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Characteristics and dynamics of a moose population in northern New Hampshire

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CHARACTERISTICS AND DYNAMICS OF A MOOSE POPULATION IN NORTHERN NEW HAMPSHIRE

BY

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THESIS

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ABSTRACT

CHARACTERISTICS AND DYNAMICS OF A MOOSE POPULATION IN NORTHERN NEW HAMPSHIRE

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Abundance indices suggest that the moose (*Alces alces*) population in northern New Hampshire has stabilized despite favorable habitat and conservative harvest. Natural mortality of unknown cause is presumed a primary reason although little is known about moose reproduction and survival in New Hampshire. This study (2002-2005) was designed to investigate the dynamics that impact this population.

Analysis of harvest reproductive data (1988-2004) indicated that average field-dressed weight of adult cows increased although corpora lutea count declined from ~1.4-1.2/cow in the study area and statewide. Yearling ovulation rate (~42%) and average weight (<211 kg) declined about 25% and 4%, respectively. Parturition of radio-marked cows ranged from 8 May-13 July (median=19 May) with 78% of births from 13-27 May. Calving rate of yearlings and adults (≥2 yr) averaged 30 and 85%, respectively, whereas twinning rate was 11%.

There were 39 mortalities (49% calves) with winterkill/parasite (41%), vehicle collision (26%), and hunting (18%) the leading causes. Radio-marked cow mortality was primarily human-related and survival was 0.87. Unmarked calf (0-2 months of age)

survival was 0.71with 76% of mortality in first month of life. Radio-marked calves (~7-12 months of age) had a survival rate of 0.67 with 74% winterkill/parasite-related mortality. Estimated annual calf survival was 0.45.

Although population modeling indicated a positive finite rate of increase (1.03-1.07), substituting lower confidence limits for winter survival of calves and both calves and yearling/adults predicted nearly stable (1.01) and negative (0.95) growth, respectively. A conservative physiological model was used to predict the metabolic impact of adult female winter ticks (*Dermacentor albipictus*) on calves over 8-weeks of engorgement. Protein deficit associated with blood loss and regeneration appeared to be the most critical problem for calves with daily losses of 30->100% of daily protein requirement over a 2-week period in moderate-severe infestations.

Unseasonably warm and snowless 2001 fall conditions likely increased transmission of ticks, therefore, winter survival of calves was lowest (0.49) and cow survival was reduced >10% in 2002. Currently, the perceived stability likely reflects the variation in survival, recruitment, and possibly low yearling fecundity caused by winter tick and more importantly tick epizootics. However, high fertility, calving rate, and body condition of adult cows, and summer calf survival should ensure local population recovery after epizootics that periodically inhibit population growth.

BACKGROUND AND STUDY DESIGN

Introduction

A once abundant moose (*Alces alces*) population was nearly extirpated in New Hampshire by the beginning of the 20th century due to unregulated hunting and loss of habitat, which compelled the State to legally protect moose in 1901 (Silver 1957). The succession of farmlands to forest in the early 1900's, the clearcutting of large acreages in the 1960's and 70's, severe winters reducing white-tailed deer (*Odocoileus virginianus*) numbers, and the continued legal protection of moose have all assisted in its comeback (Bontaites and Gustafson 1993). Approximately 6,000 moose now occupy their historic range within New Hampshire (Bontaites, moose project leader NHFG, pers. comm.). Despite the moose's return there is an absence of scientific study of its population dynamics in New England. Certain population parameters including size, growth rate, fecundity, and mortality are required to understand and predict the dynamics of a wildlife population (Caughley 1977). This information allows wildlife managers to identify and possibly influence factors regulating regional population density.

Moose provide ecological, recreational, aesthetic, and economic benefits to residents and tourists of New Hampshire. Wildlife viewing in New Hampshire generates over $341 million annually with interest in moose an important component (USFWS 2001). Revenue from moose hunting permits contributes over $200,000 annually to the New Hampshire Fish & Game Department (NHFG) while simultaneously stimulating local economic activity (NHFG 2001). Given these direct and incidental benefits, it is

imperative that this natural resource be managed effectively with sound biological data and research.

The current status of the moose population in northern New Hampshire is reasonably understood by assessing factors including annual vehicular collision and hunter reports, aerial infrared censuses (Bontaites *et al.* 2000), and analysis of biological information from harvested moose (Adams and Pekins 1995). These abundance indices suggest that the northern moose herd is no longer growing (Bontaites, pers. comm.). Substantial natural mortality of unknown cause is presumed to be the reason for this population stability. Only a single study (Miller 1989) has used radio-marked moose in New Hampshire, but it was of short duration (2 yr) and focused on habitat not population dynamics. Survival data from collared animals, particularly long-term and sex-age specific data, can greatly aid efforts to understand and predict population dynamics of moose (Modafferi and Becker 1997).

Age-specific fecundity and survival rates of moose and the underlying causes of mortality are essential to understand the population dynamics of New Hampshire's northern moose population. This research addressed these previously unknown factors and assessed their effect on the population. Moose management efforts in New Hampshire and throughout New England will benefit from this information.

Objectives

The overall goal of this study was to investigate the population dynamics of moose in northern New Hampshire through the monitoring of radio-marked moose. Specific objectives were:

1) to estimate the parturition dates, fecundity rates, and productivity of yearling and adult cow moose,

2) to analyze reproductive data from harvested cows for comparison with data from radio-marked cows,

3) to determine the causes, timing, and frequency of mortality for calf and cow moose,

4) to calculate calf and cow survival rates and quantify the influence of certain covariates on survival,

5) to predict the finite rate of increase for the population in the study area,

6) to identify factors that limit population growth of moose in northern New Hampshire, and

7) to estimate the metabolic impact of engorging female winter ticks on calves associated with blood loss.

Methods

Study Area

The study area was situated in the eastern portion of Coos County in northern New Hampshire with the majority of forestland privately owned and commercially harvested (Fig. 1). It encompassed roughly 1000 km² and included most of wildlife management units (WMU) B, C1, and C2 as designated by the NHFG. The eastern edge of WMU C2 along the Mahoosuc Range bordered the state of Maine. The core of the study area was located within the Androscoggin River watershed in the towns of Berlin, Success, Milan, Dummer, Cambridge, and Shelburne. Maintained logging roads and off-highway recreational vehicle (OHRV) trails intersected much of the forestland providing year-round accessibility. Logging roads in active timber operations were plowed during winter and many inactive logging roads and off-road vehicle trails were open to snowmobiles.

The region was dominated by high-elevation mountainous terrain bordered by lowland valleys containing a myriad of lakes, ponds, and river systems; elevation ranged from 250-1000m. The dominant cover type was northern hardwood forest consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). Boreal communities thrived in less drained sites and at higher elevation areas and were dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) (Degraaf *et al.* 1992, Sperduto and Nichols 2004). The major cover types included approximately 34% northern hardwood stands, 23% softwood stands, 17% hardwood-softwood mix, 14% clearcuts and regenerating stands of quaking aspen (*Populus tremuloides*), paper birch, and pin cherry

(*Prunus serotina*), and 10% wetlands and open water (Scarpetti *et al.*, in review). Annual ambient temperature ranged from 30 to -30°C, annual precipitation ranged from 91-123 cm; and maximum snow depth ranged from 50-70 cm at permanent monitoring sites.

The estimated moose density within management units B, C1, and C2 was 0.78 moose/km^2 or approximately 1500 moose, one of the highest concentrations of moose in New Hampshire (Bontaites, pers. comm.). Moose of both sexes were hunted annually through a permit-lottery during a nine-day period in October. An average of 115 either sex permits were assigned to the area with hunter success >85% (NHFG 2004).

Known carnivores and possible predators of moose inhabiting the study area included black bear (*Ursus americana*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). Bear densities ranged from 0.23-0.34 bear/km^2 in the region (Timmins, bear project leader NHFG, pers. comm.). White-tailed deer (*Odocoileus virginianus*) existed throughout the study area in density of 2.3-3.1 deer/km^2 (Gustafson, white-tailed deer project leader NHFG, pers. comm.).

Capture and Marking

Hawkins and Powers Aviation, Inc. (Greybull, WY) was contracted to capture moose by helicopter net-gunning (Carpenter and Innes 1995). Their personnel consisted of several animal handlers or "moose muggers", a helicopter pilot and mechanic, a wildlife veterinarian, and an emergency room physician. In addition, NHFG biologists and UNH student technicians assisted with ground support and some captures. All crewmembers were trained in proper animal handling techniques, attachment of radio-collars, and biological sampling protocol.

Captures occurred each December 2001-2003; captures were completed within

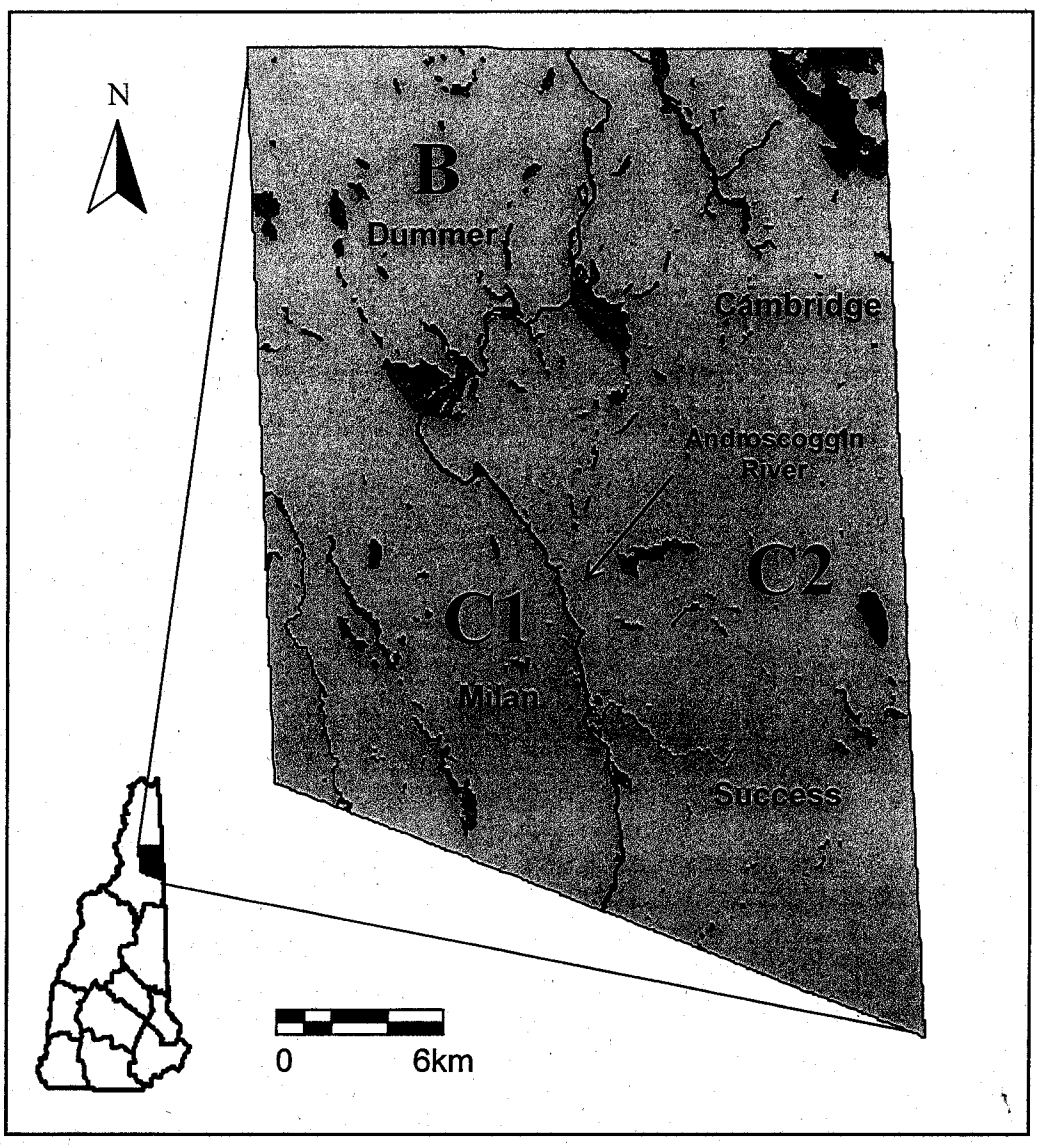


Figure 1. Study area of moose project with WMUs in Coos County New Hampshire, 2002-2005.

one-two weeks each year. Early winter months provide ideal spotting and capture conditions given adequate snow depth and lower air temperature (Carpenter and Innes 1995). Capture flights were initiated from the Berlin Municipal Airport in Milan, NH. The study area was surveyed from a fixed-wing aircraft (Cessna 152 or 172, Hamel Air, Milan, NH) for moose abundance and favorable capture sites one to two weeks prior to captures. After the first year, the primary capture sites were chosen based on the location of marked moose. An observer in a Cessna was used as a "spotter" to locate moose including radio-collared cows to capture their unmarked calves. Animals selected for capture were located proximate to clearcuts, log landings, or forest openings so that the helicopter pilot could maneuver the moose into an open area. The spotter radioed GPS-marked locations to the capture crew (two moose handlers and a net-gunner) that flew to the site in a Bell Long Ranger L-3 helicopter. When capture was not possible by net-gunning, moose were darted and immobilized with a mixture of carfentanil citrate and xylazine hydrochloride. Reversal was achieved intravenously with an antagonist mixture of naltrexone hydrochloride and tolazoline hydrochloride; moose were monitored continuously (respiration and body temperature) during the entire immobilization.

Moose were blindfolded and restrained with hobbles after capture. In 2001, 20 mL of blood was drawn from the jugular vein of cows to determine pregnancy with an assay of the pregnancy-specific protein B (PSPB, Huang *et al.* 2000) with analysis done by BioTracking, Moscow, ID. In 2002, a portable ultrasound device was used to determine pregnancy (Stephenson *et al.* 1995). The veterinarian was transported to the capture site if a moose was injured, overheated, or showed signs of capture stress. Moose were monitored every other day for two weeks to detect problems and/or mortality

related to capture stress (capture myopathy).

Both cows and calves were targeted each year. All non-calves were considered adults (≥1yr) due to the difficulty of aging moose without observing tooth wear (Peterson *et al.* 1983); calves were obvious based on relative size. Capture effort per age class was dictated by the objective to maintain 25 radio-collared adult cows each summer. Moose were fitted with VHF (n=83) or breakaway GPS (n=9) radio-collars (VHF: Model 600, GPS: Model TGW-3700, Telonics, INC., Mesa, AZ). All collars were in the 150-MHz range and contained a motion-sensitive mortality switch on a four-hour delay. Collars were sized at a circumference of 96 cm for cows. Collars were modified for calves with duct tape and medical latex which allowed for approximately 10 cm between neck and collar; after deterioration of latex and tape (~1 yr) collars eventually opened to 114 cm for bulls and 96 cm for cows (Moose Project personnel of the Michigan Department of Natural Resources, pers. comm.). Each moose was affixed with individually numbered and matched large Allflex ear tags (ALLFLEX USA Inc. Dallas, TX) distinguishing each capture year by color (2001=yellow, 2002=pink, and 2003=blue). Each tag was marked on the back with the project name and phone number. The following data were collected: GPS coordinates of the capture location, age (calf or adult), sex, apparent body condition, and presence of any accompanying moose. Samples of hair were plucked from the top of the shoulder for future analysis of metal accumulation and mineral status (Flynn *et al.* 1975); fecal pellets and obvious parasites (e.g., ticks) were also collected.

In total 92 (33 adults, 59 calves) moose were radio-marked successfully; three female calves died due to capture-related injury and one female calf escaped without a collar, but was ear-tagged (Table 1). Eleven calves born to marked cows and monitored

from birth were collared. Of the 96 total captured, 81 were net-gunned and 15 (12 adult, 3 calves) darted. Snowless conditions in 2001 resulted in 13 (33%) captures by immobilization; no animals were immobilized in December 2002 and 2003. A total of 26 cows and 14 calves were radio-marked in 2001, 4 cows and 21 calves in 2002, and 1 cow and 24 calves in 2003 (Table 1). In July 2002, two adult cows were darted and tranquilized at a roadside salt lick in Milan to redeploy GPS collars retrieved from two mortalities the previous winter.

Table 1. Age class and sex of moose radio-marked in northern New Hampshire three consecutive Decembers, 2001-2003.

		Calf		
Year	Adult cow	Male	Female	Total
2001	26	8	6	40
2002	6[a]	13	8	27[b]
2003	1	11	13	25[b]
All years	33	32	27	92[c]

[a] Includes 2 animals marked in July to redeploy GPS collars from late winter mortalities.
[b] Includes 11 calves of marked cows monitored from birth, 3 in 2002 and 8 in 2003.
[c] Does not include 3 female calves that died due to capture-related injuries and 1 female calf that escaped with ear-tags only.

Monitoring of Radio-marked Moose

Moose were relocated 1-2 times weekly with a combination of aerial telemetry, ground telemetry, and direct observation. All personnel were trained in telemetry methods as described by Mech (1983). Five monitoring seasons were defined: early

winter (16 December-15 February), late winter (16 February-15 April), spring (16 April-15 June), summer (16 June-15 September), and fall (16 September-15 December). Summer days were divided into four time periods to detect normal nocturnal and crepuscular activity in summer and possible distant movements from diurnal bedding sites; time periods were defined as feeding (0300-0900 h), bedding (0900-1500 h), feeding (1500-2100 h), and salt lick use (2100-0300 h). Use of time periods helps prevent biased sampling related to consistent diurnal relocations (Beyer and Haufler 1994).

Weekly aerial locations were attempted (Cessna, Hamel Air, Berlin Municipal Airport, Milan, NH), however, the frequency of flights was influenced by weather and season. Two side-facing H-antennas were mounted on brackets along each wing strut and connected to a switch box and TR-5 digital receiver (Telonics Inc., Mesa, AZ). Radio-collared moose were located, their final position confirmed, and then circled upon as described by Mech (1983). Visual verification was attempted when location, season, weather, and visibility were conducive to observation. Locations were recorded as waypoints (NAD-83; Universal Transverse Mercator (UTM) on a GPS (Garmin 12, Garmin Ltd. Olathe, KS). The number of moose, location, time, habitat type, distance to water, distance to forest cuttings, and moose activity (i.e., feeding, traveling, or bedding) were recorded.

Ground-based locations were performed 1-2 times weekly for each moose. R-1000 (Communication Specialists Inc., Orange, CA), TR-2, TR-3, and TR-5 receivers (Telonics Inc., Mesa, Arizona) were used with 3-element Yagi antennas (AF Antronics, Inc., Urbana, IL); RA-14 rubber duck antennas (Telonics Inc., Mesa, AZ) were used to

stalk moose. A truck-mounted non-directional whip antenna (Telonics Inc., Mesa, AZ) was used to establish the general location from maintained forest and logging roads critical to gain close proximity for accurate triangulations. A minimum of three directional bearings was taken, and at each location from which bearings were taken, UTM coordinates were recorded (Garmin GPS-12 unit). An average of 15-20 minutes elapsed between the first and last bearing; UTM coordinates and azimuth were transferred onto USGS quad maps to determine the precision of the triangulation. Triangulation data were analyzed with the LOCATE II program (Nams 2000) that uses maximum likelihood estimators to calculate animal location (Lenth 1981). All personnel were tested annually for telemetry error with a radio-collar at a known location.

Weather Measurements

Snow depth was measured weekly January-April at monitoring stations located at hardwood, softwood, mixed, regenerating, and open sites within the towns of Kilkenny and western Berlin, NH. Snow depth (meter stick) and temperature were recorded each visit. Monthly precipitation, mean ambient temperature, precipitation, snow depth, and other weather variables were available at the National Climatic Data Center's Berlin (44°27'N, 71°11'W) weather station (#270690/99999) located centrally in the study area at an elevation of 283 m.

Ambient temperature from June-August averaged 18°C reaching a high of 34°C; ambient temperature in winter (16 Dec-15 April) averaged –6.3°C with a minimum of -31°C. Daily minimum temperature in January-March was <-17.7°C for 5, 37, 29, and 27 days in 2002-2005, respectively; mean ambient temperature was -3.7, -8.4, -7.6, and -7.1°C, respectively. Annual precipitation ranged from 91.2 cm in 2002 to 122.7 cm in

2003. Mean annual snowfall was 191.8 cm and maximum recorded snow depth was 35.6, 71.1, 88.9, and 104.1 cm in 2002-2005, respectively. In December-April of 2002-2005, average weekly snow depth measured at open monitoring sites ranged from 25-50 cm and did not exceed 70 cm.

CHAPTER I

PRODUCTIVITY AND SURVIVAL

Introduction

Productivity

Natality, or the number of calves born into a moose population each year, is defined as a population's ability to increase (Odum 1959). The reproductive potential for moose is determined by the age at first reproduction, litter size, reproductive cycle length, and reproductive life. Productivity per age class yields critical information about the reproductive potential of populations; of primary importance are the fecundity rates of yearling and adult cows (Schwartz 1997). Where moose occupy good habitat their productivity and recruitment rates are high and the population can most likely endure mortality factors such as predation, disease, parasitism, severe winters, hunting, poaching, and accidental deaths. Alternatively, these sources of mortality can substantially restrict population growth in areas of poor productivity (Franzmann 2000).

The peak birthing period occurs during a short time frame between mid-May and the first week of June throughout North America (Schwartz 1997). It is hypothesized that the synchrony and timing of parturition are adaptations to long-term climactic patterns with the most favorable conditions for birth, seasonal growth, and raising offspring (Bowyer *et al.* 1998, Keech *et al.* 2000). Female condition may have a considerable effect on timing of reproduction and other life history patterns of calves. As birth weight

increases so does survival, and survival declines as birth date and litter size increase (Keech *et al.* 2000). Lower weight neonates do not compensate with increased growth for their small size and are more prone to winter mortality, increased age of first reproduction, and lower adult fertility (Keech *et al.* 1999, 2000).

Considerable variation in the age of first breeding by cows exists among moose populations. Sexual maturity is generally related to body size (Saether and Haagenrud 1983) with the majority of cows ovulating initially at 1.5 or 2.5 years of age, but cows in low quality habitat may not breed until 4.5 years (Schwartz 1997). Analysis of New Hampshire harvest data (1988-1994) indicated continuous growth by cows to 4.5 yr, significant increase in body weight from 0.5 to 1.5 yr, and a high proportion of ovulating yearlings (63%); the number of corpora lutea was correlated with weight class (Adams and Pekins 1995). Although yearling ovulation rates are good predictors of population status, not all ovulations result in pregnancy (Schwartz 1997). Studies have revealed that ovulation rates of yearlings range from 0-100% throughout North America averaging 49%, yet overall yearling pregnancy rates in the same areas were 0-62%, suggesting a fairly high ova loss (Schwartz 1997). Fecundity rates of yearling cows were 18, 41, and 64%, respectively, for above, near, and below habitat-carrying capacity across North America (Boer 1992).

Adult ovulation rates are consistently high ranging from 71-100% (Schwartz 1997); pregnancy rates compiled from studies across North America averaged 84% and ranged from 76-100% (Boer 1992). Cows can reproduce yearly until age 18 (Franzmann 1978), but the maximum productivity of cow moose probably occurs at the age of 4-7 (Sylven 1980, Saether and Haagenrud 1983, Schwartz and Hundertmark 1993).

Production can be diminished in poor habitat where females do not always produce calves in consecutive years (Albright and Keith 1987, Schwartz 1997). According to Schwartz (1992), captive cows which bred as yearlings produced fewer calves during their breeding lives (1.5 per yr) than cows that first bred at 2.5 yr. (1.9 per yr). In Sweden, yearlings with calves weighed less than yearlings without calves the following year (Saether and Haagenrud 1985). Producing offspring as a yearling appears to have negative effects on an individual's overall production and potential growth (Schwartz 1997).

Moose typically produce a singleton with twinning related to habitat quality, population carrying capacity, herd health (Franzmann and Schwartz 1985, Gasaway *et al.* 1992, Schwartz 1997), and nutritional status of the pregnant cow (Keech *et al.* 2000). There is a strong correlation between twinning rates in adult cows and yearling pregnancy rate, suggesting that similar conditions influence both (Boer 1992). Twinning rates are reported as low as 1% in South Newfoundland (Albright and Keith 1987) and as high as 88% in Rochester, Alberta (Mytton and Keith 1981). In Canada and Alaska, Gasaway *et al.* (1992) observed twinning rates of 25-90% in populations below carrying capacity, 5-25% near carrying capacity, and <5% above carrying capacity.

Fecundity is related to sexual maturation which can be affected by a myriad of ecological factors that influence physiological status of cows and ultimately ovulation, pregnancy, parturition, litter size, and calf condition (Van Ballenberghe and Ballard 1997, Keech *et al.* 2000). Fecundity and survivorship of calves determine recruitment and population trends, important factors in moose population dynamics and management (Van Ballenberghe and Ballard 1997).

Survival and Mortality

Essential to understand the dynamics of a moose population are measurements of both rates of survival and mortality, and identifying and ranking sources of mortality (Van Ballenberghe and Ballard 1997). The abundance and species of predators, weather and snow conditions, habitat availability and quality, disease, parasites, and human-related factors such as hunting, accidents, and poaching are known to influence moose survival and populations (Crichton 1987, Lankester 1987, Van Ballenberghe and Ballard 1997). While many agencies use harvest data to assess wildlife populations, these data alone are often insufficient because other mortality factors influence the population (Bender and Hall 2004). Therefore, a significant advantage of using marked populations is an increased probability of identifying environmental parameters that induce population response (DelGiudice *et al.* 1997).

Large mammal species generally display a classic U-shaped mortality curve with high mortality during the first year of life and old age, and low mortality of young adults (Caughley 1966). Radio-telemetry studies of moose have demonstrated that survival and cause-specific mortality rates may vary regionally and seasonally with age, sex, and density of moose (Van Ballenberghe and Ballard 1997). Such studies have also revealed that predators may kill high numbers of calves (Franzmann *et al.* 1980, Ballard *et al.* 1981, Larsen *et al.* 1989, Osborne *et al.* 1991, Ballard and Van Ballenberghe 1997, Keech *et al.* 2000, Bertram and Vivion 2002). Alternate prey, predator-prey ratios, and the number and diversity of ungulate predators within a moose population's range all influence the impact of predation on moose (Connolly 1978, Ballard and Van Ballenberghe 1997). However, unlike many moose populations that are impacted by

predation, New England is free of most known moose predators with the exception of black bears. Black bears primarily prey on moose calves and are not significant predators of adult moose (Ballard 1992). Bear predation is apparently independent of moose population density impacting both low and high moose populations (Ballard and Van Ballenberghe 1997).

Moose populations below habitat-carrying capacity and in areas of low predator density are probably not limited by predation (Van Ballenberghe and Ballard 1994). In regions of high predator numbers such as Alaska, predation can account for 95% of calf mortality (Bertram and Vivion 2002) and most calf mortality occurs in the first 6-8 weeks of life (Ballard *et al.* 1991, Osborne *et al.* 1991, Ballard and Van Ballenberghe 1997). Conversely, Stubsjøen *et al.* (2000) observed an 84% survival rate in areas of minimal or no predators in Norway. Black bears have removed 2-50% of radio-collared neonates, however, where predation was low, winter starvation of calves occurred at high rates in mild winters providing evidence of compensatory mortality in Alaska (Ballard and Van Ballenberghe 1997).

Winter mortality is influenced by snow conditions including depth, density, hardness, crusting, temperature, and persistence over time (Peek 1986, Franzmann 2000). Even though moose are well adapted to severe winter weather (Schwartz and Renecker 1997), snow can influence the availability of food and the mobility of animals inducing a negative energy balance (Franzmann 2000). The amount of tissue energy in body fat and protein influences survival during negative energy balance in winter (Schwartz *et al.* 1988). Calves, older adults (>8 yr), and rutted-out adult males are most likely to succumb during severe winters (Coady 1982). However, adult cows can be more

susceptible to winter mortality in response to increasing nutritional demands associated with pregnancy and lactation in long and late winters with deep snow (Schwartz *et al.* 1984, 1987a, Modafferi and Becker 1997). Snow depth of 70 cm can impede moose movement and 90 cm is indicative of conditions that reduce mobility and increase winter mortality (Coady 1974). Increased hardness or crusting of snow in open areas can also limit moose activity causing animals to seek forest stands with high canopy closure (Kelsall and Prescott 1971, Peek 1971, 1997). Not only does crusted snow impede movement and increase energetic costs, it can cause lower leg injuries (Peek 1997). Nearly 100% calf mortality was observed on the Kenai Peninsula of Alaska during winters of excessive snow depth (Franzmann 1978, 2000).

Direct mortality factors rarely act alone to influence populations. When an animal is stressed and in poor nutritional state, or during severe weather conditions, parasites potentially increase host mortality (Lankester and Samuel 1997). Moose are host to a variety of parasites and diseases (Lankester 1987), but they are rarely considered limiting factors of populations (Van Ballenberghe and Ballard 1997). The winter tick (*Dermacentor albipictus*) found on most ungulates throughout North America excluding the Arctic, has been the source of local moose die-offs, however, its potential to regulate moose populations has not been established (Van Ballenberghe and Ballard 1997, Samuel 2004).

Of all cervid hosts, moose are apparently the most severely affected by the winter tick (Welch *et al.* 1991, Samuel 2004). Infestations cause anemia, coat damage, reduced fat stores, reduced feeding, excessive grooming, restlessness, and reduced growth in calves (Samuel 2004). Nutritionally stressed animals are predisposed to carry more ticks

(Gladney *et al.* 1973) and display more signs of physiological stress (O'Kelly and Seifert 1970, Glines and Samuel 1989). More often a greater number of calves than adults die during tick-associated die-offs (Samuel 2004). March and April are months of nutritional and energetic stress for moose (Renecker and Hudson 1989) and coincide with the timing of the blood meal of adult ticks that inflicts the most irritation to the host (DelGiudice *et al.*1997). Numerous studies and reports have documented elevated moose mortality during heavy tick infestations (Anderson and Lankester 1974, Berg 1975, Samuel and Barker 1979, Blyth and Hudson 1987, Lankester 1987, Peterson 1991, Lenarz 1992, Garner and Wilton 1993, DelGiudice *et al.*1997, Samuel and Crichton 2003, Samuel 2004). The winter tick can impact moose populations and may measurably reduce juvenile recruitment and production following winters of heavy tick infestation.

The lungworm, *Dictyocaulus viviparous,* also known as the cattle lungworm, is found in various species of ruminants throughout the world and is commonly found in moose, elk (*Cervus elaphus*), and white-tailed deer in North America (Thorne *et al.* 2002). This nematode is usually not related to morbidity of moose (Lankester and Samuel 1997), although prevalent lung infections have been described in calves and yearlings (Pybus 1990; Morris, pers. comm.). *D. viviparous* is also found commonly in the small bronchioles in lungs of elk calves in winter (Thorne *et al.* 2002), and extensive emphysema occurs if large masses of worms block bronchioles (Bergstrom 1975). Severe weather conditions, poor host nutrition, or heavy tick infestations have been linked with lungworm infections and cause morbidity or death of elk (Worley 1979, Thorne *et al.* 2002).

In addition to the aforementioned sources of mortality, other factors potentially

influencing populations include incidental mortality, hunting, poaching, vehicle collision, and other forms of parasitism and disease (Van Ballenberghe and Ballard 1997). Mortality can be compensatory or additive and may fluctuate by season and area. Determining causes of mortality and whether they are limiting or regulating population growth is essential to understanding moose population dynamics.

The objective of the productivity portion of this study was to determine how parturition, yearling and adult fecundity, and twinning rates influence productivity. The main objective for the mortality portion of this study was to determine the timing, magnitude, and cause of age-specific mortality occurring in the study population. Given the lack of such data in the northeastern U.S., this information will allow managers to better interpret and predict status and dynamics of the state and provincial populations.

Methods

Productivity

To estimate calving date and fecundity rate, cows were approached on foot (walk-in) and observed at regular intervals 2-3 times weekly from 1 May-1 July, and weekly thereafter until 15 August, 2002-2005. Age class was categorized as calves <1year, yearlings ≥1 year but <2 years, and adults ≥2 years at time of breeding. The yearling sample size was unknown in 2002 (first capture year) because age could only be determined after mortality; thereafter, yearlings were recruited as captured calves.

Cows were stalked within sighting distance using telemetry homing techniques (Mech 1983). Priority was given to cows that were identified as pregnant from protein-B serum assays and ultrasound in 2002 and 2003. Attempts were made at least once weekly to observe yearlings possibly bred as calves. Parturition dates were assigned by

backdating from the estimated age of neonates; calves were aged as <1 day-old (0 days), 1 day-old, 2 day-old, 3-7 day-old (5 days), or >7 days based on coordination, mobility, wet or dry appearance, and presence of an umbilicus (Larsen *et al.* 1989). Also considered was evidence of the birth site, calf beds or tracks, and behavior and posture of cows associated with the protection or leading of their young.

Calves-at-heel were monitored for two months post-partum to measure productivity and survival. Other information recorded each walk-in included UTM GPS coordinates, weather, cow and calf behavior, surrounding habitat characteristics, and distance to logging cuts and water. Sign such as beds, tracks, fecal matter, birthing membranes, and evidence of predation was noted. Though time consuming and labor intensive, direct observation was the best method to monitor calving because observation from the air was usually hindered by dense canopy and thick vegetation typical of calving habitat in New Hampshire.

Harvest Reproductive Data

Ovaries collected from harvested animals at check stations (1988-2004) were used to measure ovulation rate and test age-specific relationships of harvested moose. Ovaries were stored in a denatured ethyl-alcohol solution and later sliced longitudinally to visually count the number of corpora lutea (CL) (Cheatum 1949b). Two age classes were considered, yearlings (≥1 yr but <2 yr) and adults (≥2 yr). Ovulation rate was calculated for each age class within the study area and statewide from 1988-2004. These data were analyzed to detect difference in distribution for all harvest years and between 1988-1998 and 1999-2004. Categories were 0 and ≥1 CL for yearlings and 0, 1, and ≥2 CL for adults. Ovulation rates were also compared with fecundity rates of study cows. Mean

field-dressed body weights were also examined for females harvested within the study area and statewide in 1988-1998 and 1999-2004. Age classes considered were 1.5, 2.5, 3.5, 4.5, 5.5, and ≥6.5 yr.

Monitoring of Unmarked Calves

Calf survival was measured during summer and post-summer periods. Summer was the 8-10 week postpartum period between 1 May-15 August. Cause-specific mortality was difficult to determine due to elapsed time between relocations, movement of collared cows, and dense vegetation. Observation of cow behavior and evidence (e.g., tracks and beds) at location sites aided to establish fate of the calf. Cows were observed ≥3 separate times after initial absence of their young until I was confident assigning mortality. The mortality date was set as the midpoint between the last observation and documentation of absence. An unmarked calf was considered a mortality if the cow died ≤2 months after birth; the mortality date of the cow was assigned to the calf. Cause of death was never determined nor remains ever located.

The post-summer period was 16 August-1 May the following year. Walk-ins to verify calf presence occurred ≥3 times for each marked cow during this period with additional observations during aerial telemetry flights. Unmarked calves were considered a mortality if a cow was observed alone; subsequent walk-ins were performed ≥3 times to confirm absence. A calf was censored for survival calculations if the dam died or survival could not be determined the following May when cows drive calves away prior to parturition. Cows separated from offspring at about 14 months in Alaska (Ballard *et al.* 1991). Calves that were subsequently collared (n=11) were included in marked survival analysis. Because monitoring was less intensive than in summer, a mortality

date was only assigned when cause and date were positively known.

Mortality Assessment of Radio-marked Moose

Mortality of each moose was monitored every 1-3 days with a combination of aerial telemetry, ground telemetry, and direct observation. Mortality was identified by a motion sensor (fast alarm pulse period at 400 msec or 150 PPM) that activated when a collar remained stationary for 4 hours. If >3 days lapsed without monitoring, a mortality check was conducted from a 45-foot fire tower located centrally within the study area (Milan State Park, Milan, NH); only the occasional moose was not detected from this location.

Ground-telemetry was used to locate a dead animal within 24 hours to confirm mortality versus a dropped collar. The site was examined for signs of predation, scavenging, human disturbance, traumatic injury, struggle, and frequency of moose activity (e.g., browsing, tracks, and beds). A GPS location and 35mm photographs were taken, and carcass condition and surrounding area were evaluated to help determine probable cause of death. First incisors were removed to determine age by counting cementum annuli on a tooth section (Matson's Laboratory, LLC., Milltown, Montana; Sergeant and Pimlott 1959, Markgreen 1969, Wolfe 1969). The mortality date was assumed to be the day the mortality pulse mode was first detected.

All moose were necropsied in the field by project technicians in 2002-2003. In 2004-2005, Dr. Richard Kingston (DVM, New Hampshire Technical Institute, Concord, NH) traveled to the study area and the NHFG Region 2 Office in New Hampton to assist with necropsies. Biologists and conservation officers of the NHFG helped to move dead moose to access roads where a truck and flatbed snowmobile trailer were used to

transport the carcass. The animal was iced-down if possible to preserve carcass condition prior to necropsy.

A customized necropsy report was used during each examination (Appendix A). Gross necropsies were performed according to techniques and procedures for large mammals (Wobeser and Spraker 1980), and necropsy samples were collected and stored according to Wobeser *et al.* (1980). The viability of samples depended on the degree of decomposition as related to the timing and cause of death. Biological samples included: first incisors, a section of liver, organ tissues (heart, liver, lung, kidney, and brain) for histology, abnormal tissues, one whole femur, ovaries, a portion or half the hide, and parasites (e.g., nematodes, ticks, and bot larvae). Sketches and notes were made of external abnormalities, trauma, parasite coverage, and hair/coat damage.

Animals were fully skinned and examined for signs of poaching, additional trauma, and parasites. All major organs were checked for abnormalities and parasites. Winter tick-associated hair loss/damage was visually documented as light, moderate, severe, or very severe (Samuel and Barker 1979, Samuel 2004); remaining tick coverage was noted. Degree of lungworm infestation and associated lung tissue damage (i.e., emphysema and congestion) was described subjectively as light, moderate, severe, or very severe.

The meninges throughout the cranium and brain were inspected for meningeal worms (Lankester and Samuel 1997). An estimate of overall body condition was based on carcass fat at the cardiac, omental, perirenal, and subcutaneous (tail, head, and brisket) regions (Kistner *et al.* 1980). Fat deposits were classified as no visible fat, slight fat, moderate fat, or heavy fat. From the whole femur, >30 g of bone marrow were extracted

to measure percent fat content oven dry weight (%FMF) (Neiland 1970). Femurs that were not collected whole were fractured and the marrow was graded visually according to Cheatum (1949a). External and internal photographs were taken of the carcass to document body condition, trauma, abnormalities, and parasites. The probable cause of death was assigned categorically as: vehicle collision, hunting, poaching, winter kill/parasite, or undetermined.

Survival Analysis

Radio-marked Moose

Known-fate modeling was implemented in program MARK v.4.2 (White and Burnham 1999, Cooch and White 2004) to estimate survival rates of radio-marked adult cows and calves and to evaluate candidate models relative to survival; this procedure is considered appropriate with data derived from radio-marked animals (White and Burnham 1999). Program MARK uses generalized linear models with a binomial error distribution and user-specified link function to generate maximum-likelihood estimates of regression coefficients and associated sampling variances. A user-specified link function and parameter index matrix (PIM) were used with each model tested. Known-fate incorporates time into survival parameters (S) by estimating the probability of survival between sampling periods or encounters. These survival estimates are analogous to rates calculated by the Kaplan-Meier product-limit estimator allowing for staggered entry of new subjects to a study (Kaplan and Meier 1958, Pollock *et al.* 1989). The fate of each radio-marked animal is assumed known at the beginning and end of each encounter occasion, therefore, survival probabilities are estimated with high precision and require fewer assumptions than apparent survival estimates (White and Burnham 1999). Known-

fate models require the following stipulations (Pollock *et al.* 1989): 1) radio-marked animals are representative of the population, 2) fates are known with certainty, 3) individual survival is independent, 4) censoring occurs independent of fate, and 5) radio-marking does not influence survival.

Field telemetry data were converted into an input file for MARK with Microsoft® Notepad v. 5.1 (Microsoft Corp. 2001). Known-fate data were separated into two sets of analyses; the first considered survival of yearling and adult cows, and the second survival of calves. Adult and yearling males were omitted from the analysis due to limited sample size (19 individuals with 6 collar losses). Analysis of radio-marked animals began three weeks after capture to exclude capture-related mortality and bias; 5 animals were excluded due to capture injury (3), capture myopathy (1), and vehicle collision (1). Adult annual survival was considered from 1 January-31 December because captures occurred in December each year. Winter survival of calves was calculated from 1 January-18 May and included animals marked at approximately 7 months of age. Calves entered the next age class on 19 May, the median birth date in the study. Adults and calves were classified into four (2002-2005) and three (2002-2004) year groups, respectively. Telemetry locations of adults were collapsed into 52 weekly intervals, and of calves into approximately 20 weekly intervals. Moose were classified as alive, dead, or censored due to collar loss, removal, or emigration at the beginning of each sampling interval. The 2005 adult analysis censored animals after 3 September due to termination of the regular monitoring schedule.

Using an information-theoretic approach, I developed a set of twenty-six and eight *a priori* candidate models to examine adult/yearling and calf survival, respectively

(Burnham and Anderson 2002) (Table 1-1). These included models that considered constant survival, weekly categorical time, year, season, interactions of year and weekly time, and year with seasons. Seasons were early winter, late winter, summer, and fall; early winter included weeks 1-7 (1 Jan-17 February), late winter included weeks 8-18 (18 February-4 May), summer included weeks 19-37 (5 May-15 September), and fall included weeks 38-50 (18 September-16 December). Weeks 51-52 were not considered as part of fall or included in seasonal analysis, but were used in calculating annual rates. Data from 2005 were not used in year models including the fall season, and weeks 36-52 in 2005 (no monitoring) were censored or fixed in the remaining models; however, apparent survival was 1.0 through 35 weeks in 2005.

Unmarked Calves

The nest-survival model in program MARK was used to estimate survival rates of unmarked calves and to evaluate relative support for covariate candidate models. This model is a type of known-fate analysis that generates point estimates of daily survival rates (DSR) and provides a means of analyzing "ragged-telemetry" data. Nest-survival is appropriate for known-fate data where the encounter occasions are not clearly delineated; the key difference between known-fate and nest-survival data types is that the exact day of animal disappearance is not known (Cooch and White 2004). Furthermore, there were walk-ins when a cow was observed without her calf yet the calf was observed during a subsequent walk-in; these data could not be classified as known-fate (White, pers. comm.).

Nest-survival, unlike known-fate, allows for variation in length of monitoring schedules. The required input data for each calf included the day it was found, the last day

Table 1-1. Known-fate candidate models used in program MARK to evaluate variation of radio-marked calf and cow moose survival (S) in northern New Hampshire, 2002-2005.

Model	Model structure	Model description
1	S(.)	S constant over time
2	S(year 02-04))	S dependent on year, 2002-2004
3	S(t)	S dependent on weekly categorical time
4	S(year*time)	Interactive effect of year and weekly time
5	S(early winter)	S dependent on the early winter season
6	S(year*early winter)	Interactive effect of year and early winter
7	S(late winter)	S dependent on the late winter season
8	S(year*late winter)	Interactive effect of year and late winter
9	S(summer)	S dependent on the summer season
10	S(year*summer)	Interactive effect of year and summer
11	S(fall)	S dependent on the fall season
12	S(year*fall)	Interactive effect of year and fall
13	S(early winter*late winter)	Interactive effect of early and late winter
14	S(year*early winter *late winter)	Interactive effect of year, early winter, and late winter
15	S(early winter*summer)	Interactive effect of early winter and summer
16	S(year*early winter*summer)	Interactive effect of year, early winter, and summer
17	S(early winter*fall)	Interactive effect of early winter and fall
18	S(year*early winter*fall)	Interactive effect of year, early winter, and fall
19	S(late winter*summer)	Interactive effect of late winter and summer
20	S(year*late winter*summer)	Interactive effect of year, late winter, and summer
21	S(late winter*fall)	Interactive effect of late winter and fall
22	S(year*late winter*fall)	Interactive effect of year, late winter, and fall
23	S(summer*fall)	Interactive effect of summer and fall
24	S(year*summer*fall)	Interactive effect of year, summer, and fall
25	S(early winter*late winter *summer*fall)	Interactive effect of early winter, late winter, summer, and fall
26	S(year*early winter*late winter*summer*fall)	Interactive effect of year early winter, late winter, summer, and fall

it was observed alive, the last day it was checked (for successful calves the last day observed alive), and fate (0=successful, 1=failed); Mark uses this information to produce an encounter history for each calf and generates maximum likelihood estimates of daily survival rate (DSR). Four groups were created, each representing an individual calving season. The four calving seasons (2002-2005) were standardized to 98 days by assuming 10 May as the first day of data collection (earliest date a calf was observed) and 15 August as the last day (end of the neonatal monitoring season). For calves with fate unknown at 60 days (i.e., late born calves), data were only included to the day fate was certain. The nest-survival model provides an estimation of total calf survival from day one to 60 days as a product of DSR over that period.

Models incorporating constant survival, year, covariates of calf age and birth date, and additive models of year with age and birth date were used to test calf survival (Table 1-2). Constant survival rate in MARK is equivalent to Mayfield nest success (Mayfield 1961) as modified by Johnson (1979). A user-specified link function and parameter index matrix (PIM) was used for each model tested and a design matrix (DM) was incorporated for age, season date, and birth date models. Assumptions of the daily nest-survival model were: 1) calves were accurately aged when found, 2) homogeneity of daily survival rates, 3) calf fates were positively determined, 4) walk-ins did not influence survival, and 5) calf fates were independent.

Both known-fate and nest-survival models were evaluated and ranked with Akaike's Information Criterion adjusted for small sample size (AIC_c). AIC uses a model selection procedure that indicates those models that best fit the data with the fewest parameters. Comparison between models was made with the ΔAIC_c values, which is the

expected difference between each model and the best model or models with lowest AIC_c value. Models were further differentiated by their ΔAIC_c weights, which is the relative likelihood that the model is the best of the candidate models relative to the data and sampling design. Models with ΔAIC_c weights ≤ 2 received substantial empirical support, those with weights of 4-7 received less empirical support, and models with weights >10 received no empirical support (Burnham and Anderson 2002).

Table 1-2. Nest-survival candidate models used in program MARK to evaluate variation of unmarked calf survival (S) in northern New Hampshire, 2002-2005.

Model	Model structure	Model description
1	S(.)	S constant over time
2	S(year)	S dependent on year
3	S(calf age)	S dependent on calf age
4	S(year+calf age)	Additive effect of year and calf age
5	S (birth date)	S dependent on birth date
6	S(year+birth date)	Additive effect of year and birth date

Statistical Analysis

Median parturition dates among years were analyzed with a Tukey-type multiple comparison median test (Zar 1999). Chi-square tests of independence were used to compare corpora lutea (CL) counts and mean cow weights were examined using a general linear model (GLM) followed by Tukey's test for multiple comparison of means as part of the annual New Hampshire moose harvest data (1988-2004) statewide and in management units B, C1, and C2 (Zar 1999). Intraspecific variation in sources of mortality were compared among age classes with Chi-square goodness-of-fit tests. A

Chi-square goodness-of-fit test was used to determine variation in timing of unmarked neonatal losses. Analysis was performed with SYSTAT v. 10 (SPSS Inc., 2000); results were considered statistically significant at $p < 0.05$ and $\alpha = 0.05$.

Results

Pregnancy Rates

In 2002, 15 of 24 cows (63%) tested pregnant by blood assay (PSPB), and 13 of the 15 (87%) were subsequently observed with a calf. Of the 9 cows that tested negative, 4 were winter mortalities aged 1.5, 6.5, 12.5, and 15.5 years with no observed fetuses; the 5 that survived to calving season included one cow observed with calf and 3 known yearlings. The four cows captured in 2003 were identified as pregnant by ultrasound and all were subsequently observed with a calf. The overall pregnancy rate was 68%; 78% in adult cows and 20% in yearlings.

Parturition Dates

Estimated birth dates (n=77) indicated that parturition ranged from 8 May-13 July with a median date of 19 May (Fig. 1-1). The same cow had two July births; no other births were recorded beyond June. The annual median parturition date ranged from 17-22 May and birthing was highly synchronous with 78% of births occurring from 13-27 May and 10% beyond 31 May. The annual calving season averaged 42 days in length ranging 22-62 days long. Timing of parturition was similar among years (Tukey-type multiple comparison median test, $\alpha = 0.05$). The mean estimated age at first observation (n=86) was 2.1 d (SD=1.9); only one calf was aged at >1 week old.

Productivity

The overall calving rate (cows that gave birth/total cows) was 75% (79 of 106) for

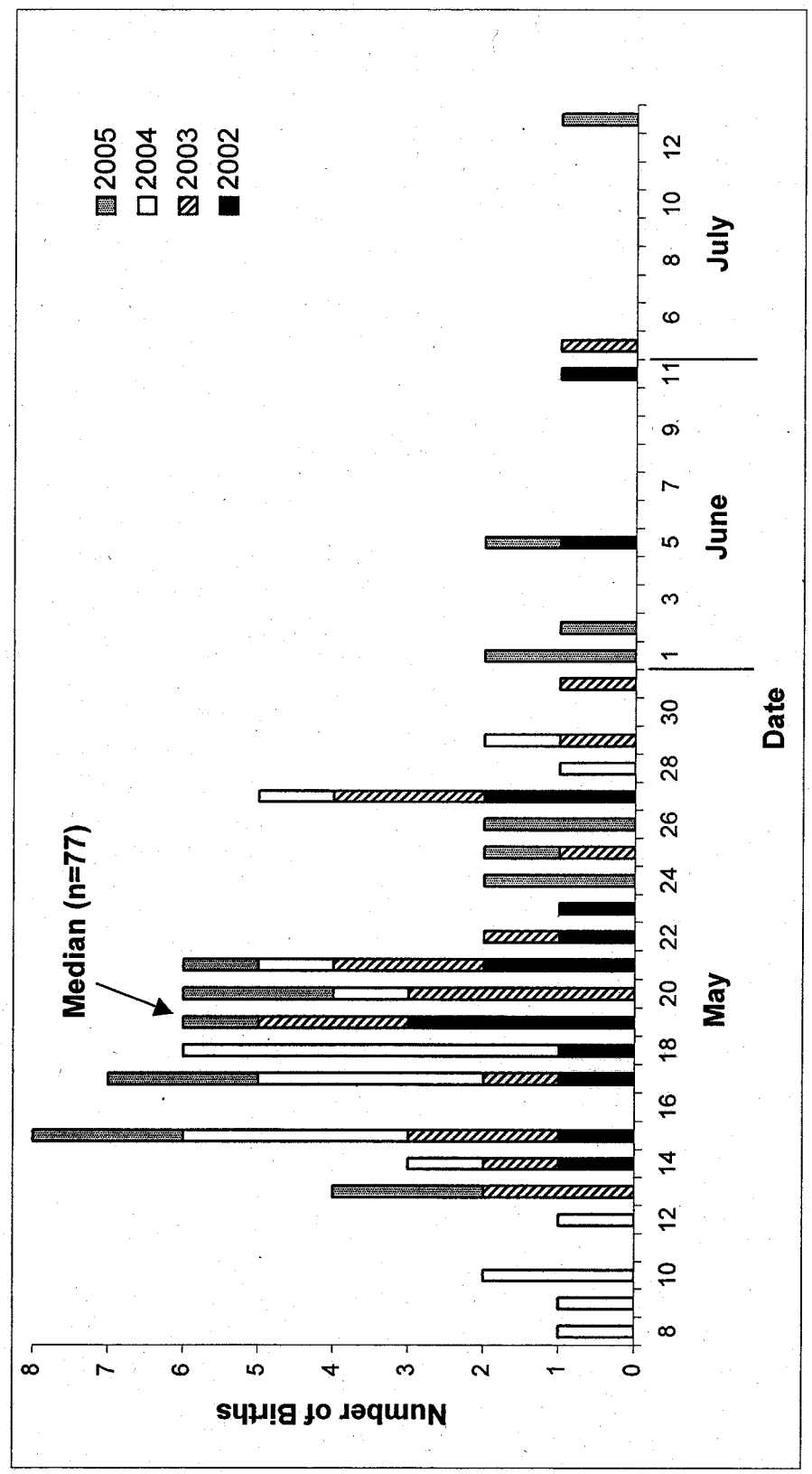


Figure 1-1. Observed timing and parturition of cow moose in northern New Hampshire, 2002-2005.

Table 1-3. Annual and total observed reproduction of radio-marked yearling and adult cow moose in northern New Hampshire, 2002-2005.

Year	Sample (n)			Calving rate %			Twinning rate %		
	Yearling	Adult	Total	Yearling	Adult	Total	Yearling	Adult	Total
2002	5	17	22	20	82	68	0	21	20
2003	1[a]	26	27	100	77	88	0	10	10
2004	5	24	29	0	92	78	0	9	9
2005	9[a]	19	28	44	89	74	25	6	10
All years	20	86	106	30	85	75	17	11	11

[a] Both 2003 and2005 include a yearling that dropped its collar but was observed with a calf.

yearling and adult cows combined in 2002-2005 (Table 1-3). Annual calving rates of yearlings and adults averaged 30 and 85%, ranging from 0-100% and 77-92%, respectively; no calves were known to reproduce. Average fecundity (total calves/total cows) was 0.35 and 0.94 for yearlings and adults, respectively. Twenty-eight adult cows were observed more than one calving season; 21 (75%) had a calf in consecutive years. Fourteen adult cows were observed each calving season and 7 had a calf each of the 4 years; annual production for these 14 cows averaged 0.96 calves/cow. The overall twinning rate (cows observed with twins/cows observed with at least one calf) was 11% ranging 9-20% annually. Of the 9 sets of twins observed, 2 adult cows had twins in multiple years (2 and 3 years), and one yearling was observed with twins.

Harvest Reproductive Data

The statewide ovulation rate of yearlings in 1988-2004 (n=387) was 48% with an average CL count of 0.53 (SD=0.60), similar to rates of 51% and 0.54 (SD=0.58) CL within the study area (n=93, Table 1-4). Adults (n=238) in the study area averaged 1.33 (SD=0.68) CL, similar to the statewide (n=1001) average of 1.29 (SD=0.63) CL. Average adult cow age in the study area was 4.6 yr in 1988-1998 and 5.5 yr in 1999-2004; statewide age also increased from 4.5 to 5.2 yr.

Yearling ovulation rates declined from 56 to 42% in the study area from 1988-1998 (n=55) to 1999-2004 (n=38), but there was no difference in the distribution of CL counts (0 and $\geq$1) in those time periods (χ^2=1.83; df=1; p=0.176). The CL count per yearling declined from 0.62 (SD=0.62) to 0.42 (SD=0.50) CL. The statewide ovulation rate of yearlings similarly declined from 56 to 41% but a difference was observed in CL distribution (χ^2=9.48; df=1; p=0.002); the related CL count per yearling declined from

Table 1-4. Ovulation and corpora lutea (CL) data from harvested cow moose in New Hampshire, 1988-2004.

Parameter	Yearlings					Adults				
	n	0 CL	1 CL	≥2 CL	% Ovulated	n	0 CL	1 CL	≥2 CL	% Ovulated
1988-1998										
Units B, C1, and C2	55	24	29	2	56	104	7	52	45	93 (46)[a]
Statewide[b]	187	82	89	16	56	492	38	253	201	92 (44)
1999-2004										
Units B, C1, and C2	38	22	16	0	42	134	12	75	47	91 (39)
Statewide[b]	200	119	78	3	41	509	43	314	152	92 (33)
All years										
Units B, C1, and C2	93	46	45	2	51	238	19	127	92	92 (42)
Statewide	387	201	167	19	48	1001	81	567	353	92 (38)

[a] Percent of bred adults with ≥2 CL.
[b] Significantly different between time periods in statewide CL distribution within yearling and adult age classes.

Table 1-5. Mean and standard deviation of field-dressed body weights (kg) of harvested cow moose in New Hampshire, 1988-2004.

Age class	Statewide		Units B, C1, and C2	
	1988-1998	1999-2004	1988-1998	1999-2004
1.5	213±32.0 (155)[a]	204±25.8 (269)	218±25.8 (52)	210±24.0 (57)
2.5	250±34.9 (149)	256±31.3 (206)	257±31.3 (35)	261±27.3 (59)
3.5	257±34.7 (91)	274±36.6 (164)	263±33.5 (20)	282±36.1 (46)
4.5	271±34.9 (51)	296±43.3 (142)	279±34.5 (19)	309±37.1 (31)
5.5	262±32.4 (44)	294±51.0 (80)	300±29.4 (5)	316±46.9 (22)
≥6.5	261±35.0 (94)	299±52.4 (214)	263±27.1 (24)	303±47.1 (65)

[a] Sample size.

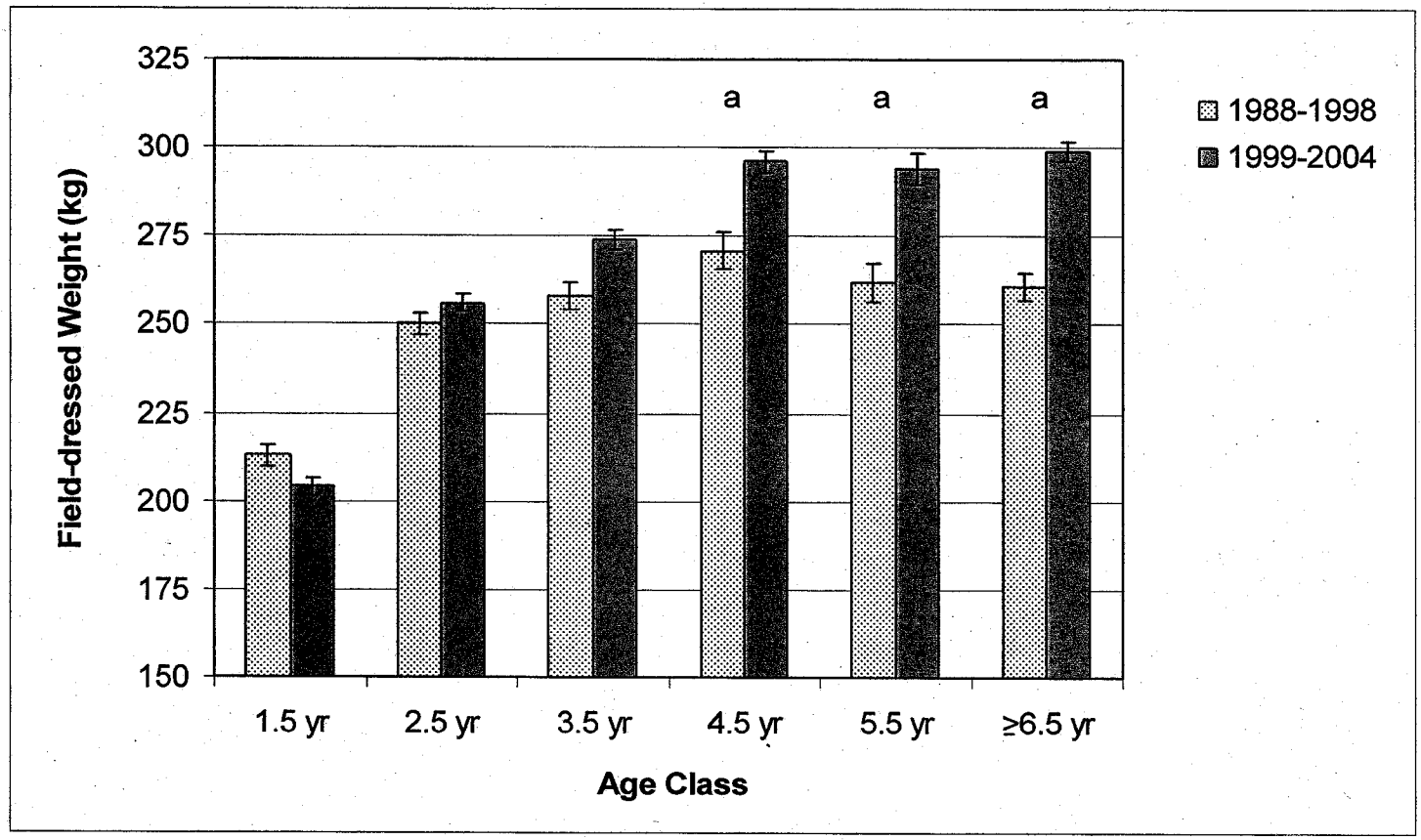


Figure 1-2. Mean (±SE) field-dressed body weight (kg) of harvested cow moose in New Hampshire, 1988-2004. a-significantly different between 1988-1998 and 1999-2004 within age class.

0.65 (SD=0.65) to 0.42 (SD=0.52) CL. There was also no difference detected in the distribution of CL counts (0, 1, and ≥2) for adults in the study area in 1988-1998 (n=104) and 1999-2004 (n=134) (χ^2=1.77; df=2; p=0.412). Adult ovulation rates remained similar at 93 and 91%, although the percentage of cows with ≥2 CL declined from 46 to 39%. The number of CL per adult declined from 1.44 (SD=0.74) to 1.24 (SD=0.61) CL. Statewide, adults had a similar ovulation rate of 92% in both time periods and a decline from 44 to 33% of cows with ≥2 CL, although there was a difference in CL count distribution (χ^2=13.38; df=2; p=0.001) (Table 1-4); CL per adult declined from 1.36 (SD=0.67) to 1.22 (SD=0.59) CL.

Overall mean field-dressed weight was different for like age classes between time periods 1988-1998 and 1999-2004 (p<0.05). Weight between cows in the study area and statewide were not different between time periods (p>0.05), therefore weights were analyzed statewide. Comparisons with Tukey's test showed a difference for 4.5 yr, 5.5 yr, and ≥6.5 yr old cows between time periods (P≤0.018), while no difference was observed for 1.5 yr, 2.5 yr, and 3.5 yr olds (p≥0.068). Mean weight of yearling cows declined about 4% in the study area (218 to 210 kg) and statewide (213 to 204 kg) from 1988-1998 to 1999-2004. The percentage of yearlings ≥200 kg declined slightly from 77 to 75% and 68 to 64% in the study area and statewide, respectively. Mean body weights of 2.5 to ≥6.5 yr old cows increased between time periods both in the study area and statewide with each age class displaying a similar increase (Figure 1-2). Mean body weight of 3.5 yr old cows increased 19 and 17 kg in the study area and statewide, whereas, 4.5 yr old cows increased 30 and 25 kg, respectively (Table 1-6).

Unmarked Calf Survival

Eighteen calves in 2002, 22 in 2003, 24 in 2004, and 22 in 2005 were monitored during the four calving seasons. Of the 86 calves, 71% survived approximately 60 days to August 15. Calf survival was known only to 30 days for one calf born in July 2005, and singleton calves of 3 GPS-marked cows that had their collars removed in June 2004; apparent summer survival (calves surviving/calves born) ranged from 0.55-0.81. Most mortality (76%) occurred ≤28 days post-parturition (Fig. 1-3). A difference in the total number of mortalities was found between the intervals of 0-28 (n=19) and ≥29 days (n=6) (χ^2=6.76; df=1; p=0.009). One set of twins was lost and four of the 9 total sets of twins had one loss. Four cows lost a calf in more than one summer season; 2 cows lost a calf in 3 of 4 summers.

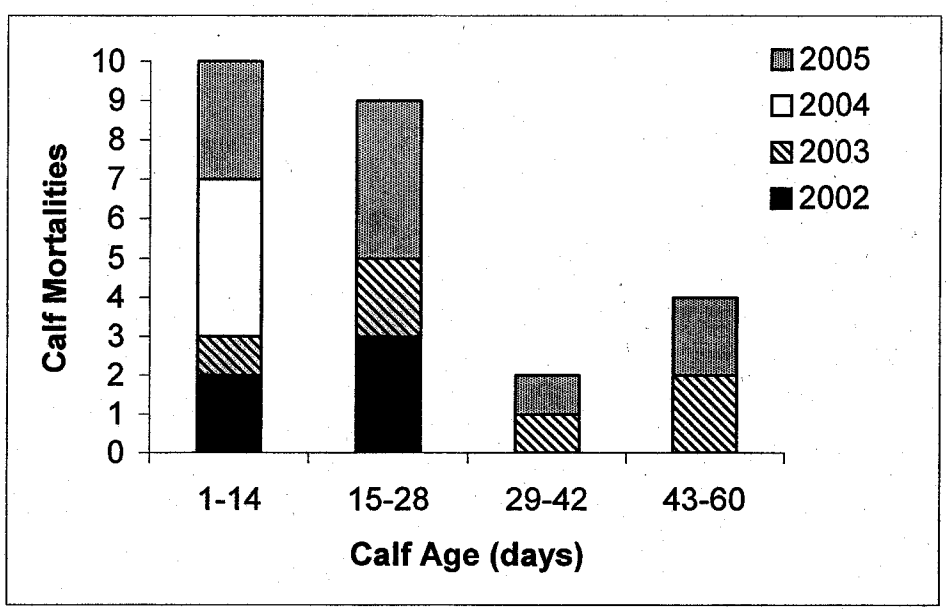


Figure 1-3. Age of mortality of unmarked calves (born to marked cows) during summer (1 May- 15 August) in northern New Hampshire, 2002-2005.

Thirty calves monitored in three post-summer periods (2002-2004) had an overall apparent survival rate of 0.80, ranging 0.67-0.91 annually; one death by vehicle collision was confirmed. Combining summer and post-summer estimates yielded an approximate estimate of annual survival of 0.57.

Cause-specific Mortality of Radio-marked Moose

The status (active, dropped collar, or mortality) of all but 1 of 92 radio-marked moose was known at project termination (Appendix C). Seventeen moose (9 calves, 3 yearlings, and 5 adults) lost their collars and 5 GPS-collars were programmed to open for retrieval. There were 39 mortalities (19 calves, 6 yearlings, and 14 adults; Table 1-6, Appendix A) with 41% occurring in April and 21% in October (Fig. 1-4). Calves, yearlings, and adults comprised 49, 15, and 36% of mortalities, respectively. Calf mortality rate was lower for females (30%) versus males (44%). Yearling and adult bulls represented, on average, 6 individuals (~20%) in the annual marked population and comprised only 10% of the overall mortality. Cause-specific mortality of calves was statistically associated with winterkill/parasite (74%) (χ^2=24.58; df=3; p=0.00002). There was no relationship identified in yearlings and adults (χ^2=7.26; df=3; p=0.064).

The fate of only 7 calves was documented in 2002 because of dropped collars; ≥20 calves were monitored in 2003 and 2004. Winterkill/parasite was the most common cause of mortality (41%) (Tables 1-6, 1-7); twelve deaths (75%) occurred in April with the others in February (1), March (2), and May (1) (Table 1-8). Calves represented most of this mortality (88%) with 57, 25, and 27% of calves dying in 2002, 2003, and 2004, respectively. Two adult cows (6.5 and 15.5 yr) and 14 calves were necropsied and documented as malnourished, infested with winter ticks, and with varying degrees of hair

loss/damage; 9 of the calves had lungworm infestations (Table 1-8). Hair loss/damage of 2 adult cows and 4 calves was classified as moderate-very severe in 2002. In 2003, 5 calves were classified as moderate tick/moderate lungworm (2), moderate tick/light lungworm (1), light tick/moderate lungworm (1), and moderate tick (1). In 2004, 5 calves were classified as severe tick/moderate lungworm (1), moderate tick/moderate lungworm (3), and light tick/moderate lungworm (1). The mean %FMF for this mortality source was 15.6% (SD=8.1, range=10.1-41.1%); 13 of 15 were ≤15.5% (n=15, Table 1-8). Vehicle collisions (n=10) accounted for 26% of mortality with 1-3 deaths annually; 50% occurred in May-June and 60% occurred near salt licks (Fig. 1-4). Two, 2 year-old cows emigrated from the study area and were killed in June and October 2004 on Interstate 95 near Kennebunk, Maine approximately 160 km from the core of the study area. Vehicle-killed animals appeared to be in adequate health and not predisposed to other injuries or disease. Hunting accounted for 18% of the overall mortality with 5 adult cows, 1 adult bull, and a yearling bull harvested within the study area. One adult cow was harvested in Maine at the fringe of the study area after removal of its GPS collar. Hunting represented 31% of all yearling and adult cow mortalities and 50% of yearling and adult bulls. Five (13%) mortalities were classified as undetermined. In 2002, an adult (12.5 yr) and yearling cow died during April, but had light hair loss and little tick evidence, fair fat deposits, >52% FMF, and were not pregnant. Also, a malnourished adult cow that successfully calved died in June. A malnourished yearling bull died in December 2003 with no observed trauma. A calf in April 2004 was scavenged with only scattered bones and hide remaining at the site. Given the month and 13.4 % FMF, it was most likely a winterkill/parasite mortality.

Table 1-6. Age- and sex-related mortality and collar loss of radio-marked moose in northern New Hampshire, December 2001-August 2005.

Parameter	Adult		Yearling		Calf[a]		Total	
	Male	Female	Male	Female	Male	Female	n	%
Collar drops[b]	3	2	3	0	4	5	17	18
Mortality source								
Capture myopathy	0	0	0	0	1	0	1	2
Hunting[c]	1	5[d]	1	0	0	0	7	18
Vehicle collision	0	4[d]	1	2	2	1	10	26
Winterkill/parasite	0	2	0	0	8	6	16	41
Undetermined	0	2	1	1	1	0	5	13
Total mortalities	1	13	3	3	12	7	39	42

[a] Calves at approximately 7 months of age when collared.
[b] Moose that lost their radio-collars due to premature collar expansion, over-sized collar, or faulty attachment.
[c] No study moose were reported to check stations in 2005 although monitoring ended before 2005 hunt.
[d] Includes one collar drop.

Table 1-7. Cause-specific mortality of radio-marked moose in northern New Hampshire, December 2001-August 2005.

Mortality source	2002		2003		2004		2005		All years	
	n	%	n	%	n	%	n	%	n	%
Capture myopathy	1	7	0	0	0	0	0	0	1	2
Hunting[a]	1	7	2	18	4	31	0	0	7	18
Vehicle collision	3	21	3	27	3	23	1	100	10	26
Winterkill/parasite	6	43	5	46	5	38	0	0	16	41
Undetermined	3	21	1	9	1	8	0	0	5	13
Total mortalities	14	-	11	-	13	-	1	-	39	-

[a] No study moose were reported to check stations in 2005 although monitoring ended before 2005 hunt.

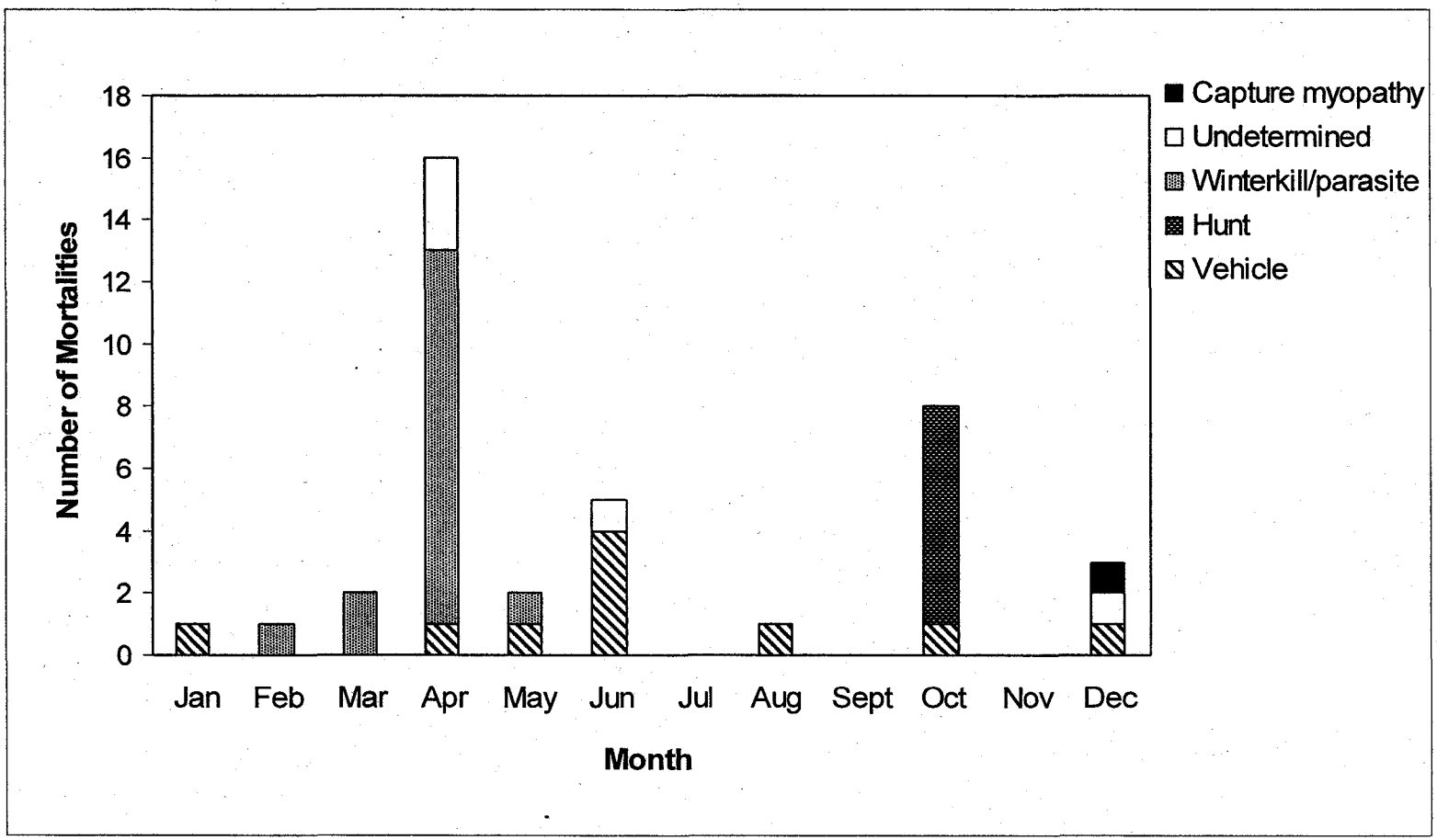


Figure 1-4. Monthly cause-specific mortality of radio-marked moose in northern New Hampshire, December 2001-August 2005.

Table 1-8. Assessment of radio-marked moose categorized as winterkill/parasite mortalities in northern New Hampshire, 2002-2004.

ID	Sex	Mortality date	Age	Hair loss/ coat damage	Lungworm infestation	%FMF	Body fat condition
9	M	27Apr02	Calf	Very severe	None[a]	14.5	No fat
16	F	18Apr02	15.5	Moderate	None	10.7	No fat
28	F	20Apr02	6.5	Severe	None	12.4	No fat
41	F	30Mar02	Calf	Severe	None	11.1	No fat
42	M	18Apr02	Calf	Very Severe	None	12.5	No fat
45	M	20Feb02	Calf	Moderate	None	-	Slight fat
130	M	19Apr03	Calf	Moderate	Light	41.1	Slight fat
136	F	11Apr03	Calf	Light	Moderate	15.4	No fat
146	M	09Apr03	Calf	Moderate	Moderate	11.2	No fat
148	M	27Mar03	Calf	Moderate	Moderate	11.3	No fat
150	F[b]	09Apr03	Calf	Moderate	None	27.6	Slight fat
156	F	28Apr04	Calf	Moderate	Moderate	13.7	No fat
158	M	30Apr04	Calf	Moderate	Moderate	14.6	No fat
165	M	05May04	Calf	Moderate	Moderate	15.5	No fat
171	F	14Apr04	Calf	Light	Moderate	13.7	No fat
174	F	20Apr04	Calf	Severe	Moderate	12.3	No fat

[a] No animals were observed with lungworms in 2002.
[b] Bot larvae infestation in pharynx.

Survival Analysis

Radio-marked Cows

The best-fitting model for adult cows was S(year 2002-2004) (AIC_c weight=0.249) which indicated that survival was year-dependent or had annual variation (Table 1-9). Derived annual survival estimates were 0.74 (SE=0.08, 95% CI=0.55-0.87) in 2002, 0.87 (SE=0.06, CI=0.70-0.95) in 2003, and 0.91 (SE=0.05, CI=0.74-0.97) in 2004. Model S(year*early winter*late winter) received substantial support as the second best model indicating that variation in survival was related to the interaction of early winter, late winter, and year (ΔAIC_c =1.374 and AIC_c weight=0.125). Variation was most likely due to no mortality observed in the early winter season and that late winter of 2002 had the lowest seasonal survival observed in the study. The remaining models received little to no support as all had ΔAIC_c values >2 (Table 1-9). The two models incorporating weekly categorical time performed poorest. Adult seasonal survival estimate as a product of weekly estimates ranged from 0.94 (SE=0.03) in fall to 1.0 (SE=0.00) in early winter; overall adult survival for the study was 0.87 (SE=0.03) (Table 1-10). Adult weekly survival rate was the lowest in late winter 2002 (0.88). Other period trends with lower weekly survival for all years occurred in weeks 24-25 of June during summer and weeks 41-43 of October during fall (Fig. 1-5).

Radio-marked Calves (~7-12 months of age)

The best-fitting model for calves was S(late winter) which indicated variation in survival for all years between late winter and remaining weeks consisting of early winter and first 2 weeks of summer prior to entering the yearling age class (AIC_c weight=0.848) (Table 1-11). This model estimated the probability of surviving the 20-week monitoring

period (1 January-18 May) as 0.70 (SE=0.06, 95% CI=0.57-0.81). The next best model, S(t), addressed weekly time and received little support (ΔAIC_c=4.387 and AIC_c weight=0.095). There was little to no support for remaining models which had ΔAIC_c values >6. Although no relationship was detected in survival rates of calves in model analysis between years, the derived estimate in 2002 was 0.49 (SE=0.19, CI=0.18-0.82), 0.71 (SE=0.10, CI=0.49-0.87) in 2003, and 0.68 (SE=0.10, CI=0.47-0.84) in 2004. The highest percentage of calves died in 2002, but high collar loss that year weakened the precision of estimates. There was a trend in weekly survival among years where weeks 13-18 (25 March-4 May) had the lowest survival, and only one mortality was observed during the early winter (Fig. 1-6). Overall, calf survival (n=57) from ~7-12 months of age as a product of the 20 weekly estimates (1 January-18 May) was 0.67 (SE=0.07; Table 1-11).

Unmarked calves (0-2 months of age)

Constant daily calf survival (i.e., Mayfield estimator) was 0.9943 from model S(.) and assuming constant DSR, overall calf survival was 0.71(SE=0.05, 95% CI=0.61-0.80) to 60 days for all years pooled. Annual rates calculated by model S(year) were 0.73 (SE=0.10, CI=0.47-0.88) in 2002, 0.75 (SE=0.09, CI=0.53-0.88) in 2003, 0.81 (SE=0.08, CI=0.58-0.93) in 2004, and 0.55 (SE=0.10, CI=0.33-0.73) in 2005; no annual difference in DSR was found. Other candidate models better explained the variation in calf survival (Table 1-12). The best-fitting model, S(calf age), indicated variation in DSR with calf age (AIC_c weight=0.584). This model displayed a linearly increasing trend in calf survival as a calf ages with a positive slope for logit DSR; β=0.025 (SE=0.01) (Fig. 1-7). The next best model, (year+calf age), an additive effect of year and calf age received

Table 1-9. Ranking of known-fate models in program MARK for radio-marked yearling/adult moose survival in northern New Hampshire, 2002-2005.

Adult known-fate model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight[c]	K[d]	Deviance[e]
S(year 2002-2004)	191.176	0.000	0.249	3	74.598
S(year*early winter*late winter)	192.550	1.374	0.125	9	63.942
S(year*fall)	193.230	2.054	0.140	6	70.640
S(early winter)	193.596	2.420	0.074	2	79.020
S(year*late winter*fall)	193.890	2.714	0.064	9	65.282
S(year*late winter)	194.205	3.029	0.055	8	67.604
S(early winter*fall)	194.478	3.302	0.048	3	77.900
S(year*summer*fall)	194.934	3.758	0.039	9	66.326
S(early winter*late winter*summer*fall)	195.381	4.205	0.038	4	76.799
S(year*early winter*fall)	195.555	4.379	0.030	9	66.947
S(early winter*late winter)	195.567	4.390	0.028	3	78.988
S(.)	195.987	4.811	0.028	1	83.412
S(fall)	196.070	4.894	0.022	2	81.494
S(year*early winter*late winter*summer*fall)	196.161	4.985	0.022	12	61.527
S(late winter*fall)	196.995	5.819	0.021	3	80.417
S(year*early winter)	197.066	5.890	0.014	8	70.465
S(late winter)	197.719	6.543	0.013	2	83.142
S(summer)	197.874	6.698	0.009	2	83.298
S(summer*fall)	197.986	6.810	0.009	3	81.408
S(year*early winter*summer)	198.345	7.169	0.007	9	69.737
S(late winter*summer)	199.707	8.531	0.004	3	83.129
S(year*summer)	200.815	9.638	0.002	8	74.213
S(year*late winter*summer)	201.378	10.202	0.002	12	66.744
S(t)	241.991	50.815	0.000	52	26.359
S(year*t)	507.037	315.841	0.000	191	0.000

[a] Akaike's information criterion corrected for small sample size.
[b] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[c] Akaike's model weight.
[d] Number of estimable parameters.
[e] Difference in –2log(Likelihood) of the current model and Difference in –2log(Likelihood) of saturated model.

Table 1-10. Survival rates generated from weekly estimates in known fate analysis of program MARK, for radio-marked calves (~7-12 months of age) and yearling/adult cows in northern New Hampshire, 2002-2005.

	Adult			Calf		
Season	S[a]	SE	95% CI	S	SE	95% CI
Early winter 1 Jan-17 Feb	1.000	0.000	1.000-1.000	0.983	0.017	0.888-0.998
Late winter 18 Feb-4 May	0.963	0.018	0.906-0.986	0.701	0.065	0.561-0.811
Summer 5 May-17 Sept	0.957	0.019	0.902-0.982	-	-	-
Fall 18 Sept-16 Dec	0.940	0.026	0.864-0.975	-	-	-
Overall[b]	0.866	0.033	0.786-0.920	0.668	0.066	0.550-0.800

[a] Seasonal survival rates are a product of weekly estimates.
[b] A total of 52 weeks for adults and 20 weeks for calves.

Table 1-11. Ranking of known-fate models in program MARK for radio-marked calf (~7-12 months of age) moose survival in northern New Hampshire, 2002-2004.

Calf known-fate model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight[c]	K[d]	Deviance[e]
S(late winter)	166.610	0.000	0.848	2	50.453
S(t)	170.997	4.387	0.095	20	17.995
S(year*late winter)	172.928	6.319	0.036	6	48.699
S(.)	174.282	7.673	0.018	1	60.134
S(year)	178.061	11.451	0.002	3	59.892
S(year*t)	239.932	73.322	0.000	60	0.000

[a] Akaike's information criterion corrected for small sample size.
[b] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[c] Akaike's model weight.
[d] Number of estimable parameters.
[e] Difference in –2log(Likelihood) of the current model and Difference in –2log(Likelihood) of saturated model.

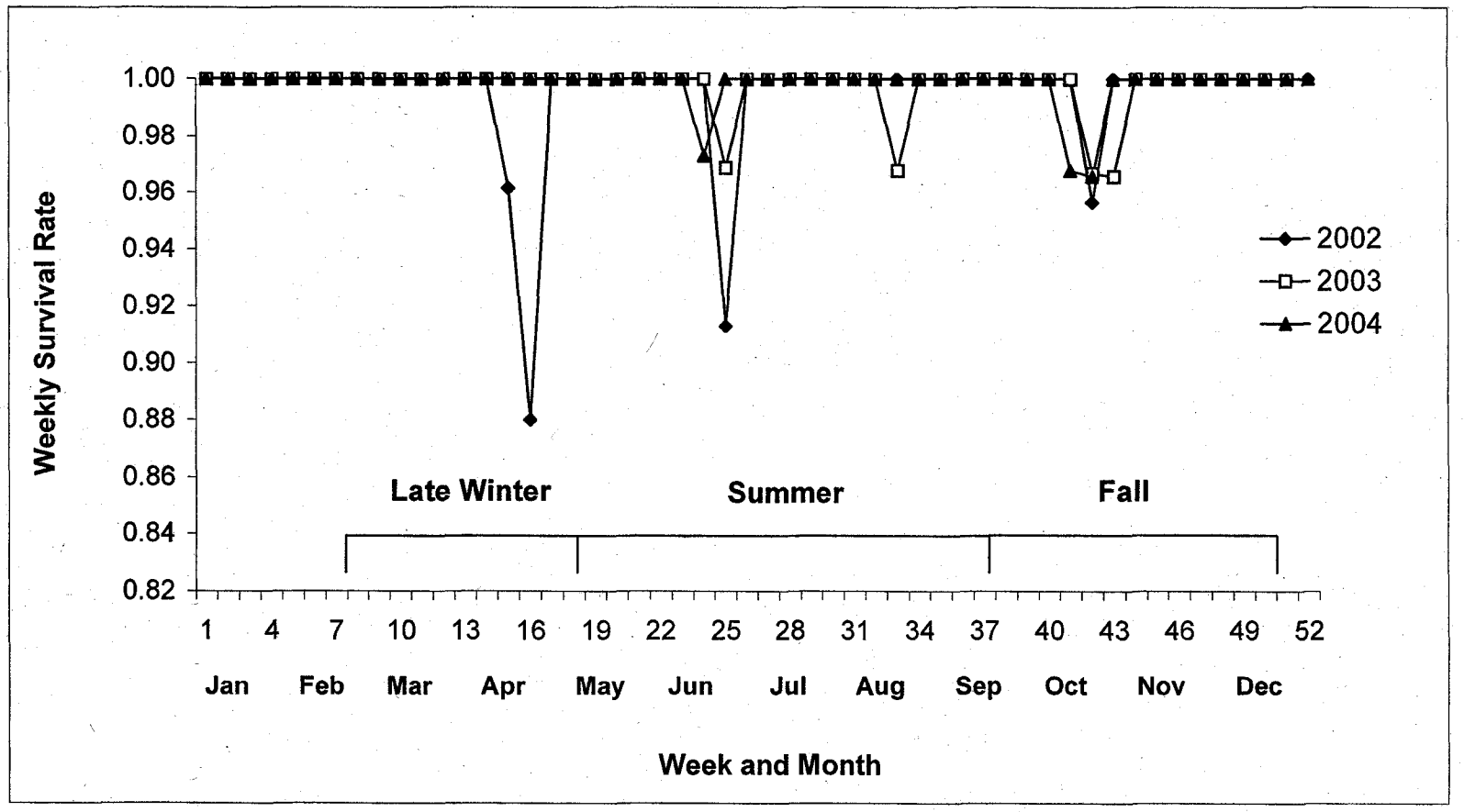


Figure 1-5. Weekly survival rates generated in program MARK for radio-marked cows in northern New Hampshire, 2002-2004. Weeks beginning 1 January and survival was 1.0 for weeks 1-35 in 2005.

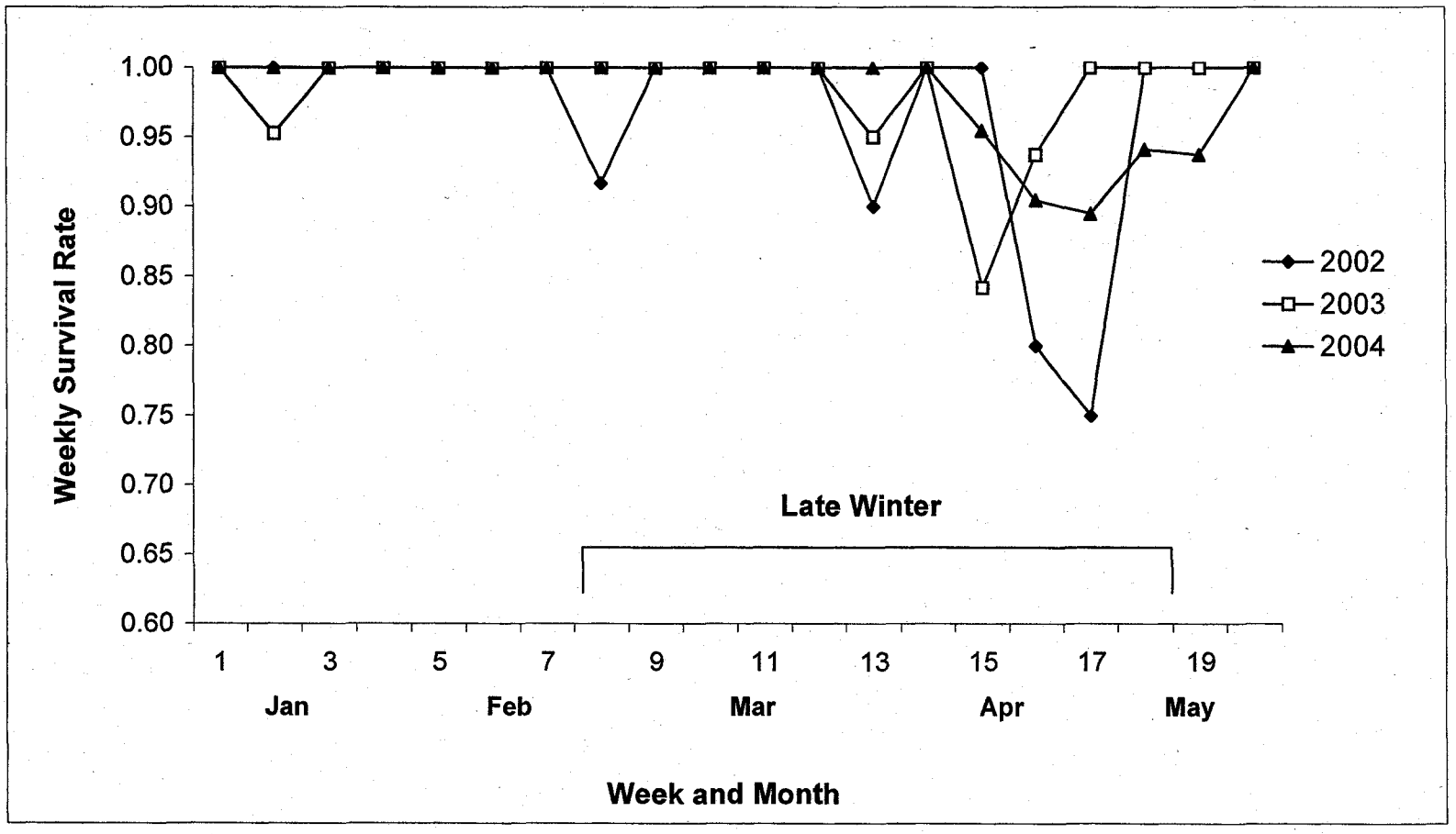


Figure 1-6. Weekly survival rates (1 January- 18 May) generated in program MARK for radio-marked calves (~7-12 months of age) in northern New Hampshire, 2002-2004.

Table 1-12. Ranking of nest-survival models in program MARK for unmarked calf moose survival to 60 days of age in northern New Hampshire, 2002-2005.

Nest-survival model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight[c]	K[d]	Deviance[e]
S(calf age)	186.573	0.000	0.584	2	182.570
S(year+calf age)	188.841	2.269	0.188	5	178.827
S(.)	189.844	3.272	0.114	1	187.843
S(birth date)	191.501	4.928	0.050	2	187.498
S(year)	191.855	5.283	0.042	4	183.846
S(year+birth date)	192.979	6.406	0.024	5	182.964

[a] Akaike's information criterion corrected for small sample size.
[b] Difference between $AIC_{c(i)}$ and minimum AIC_c observed.
[c] Akaike's model weight.
[d] Number of estimable parameters.
[e] Difference in –2log(Likelihood) of the current model and Difference in –2log(Likelihood) of saturated model.

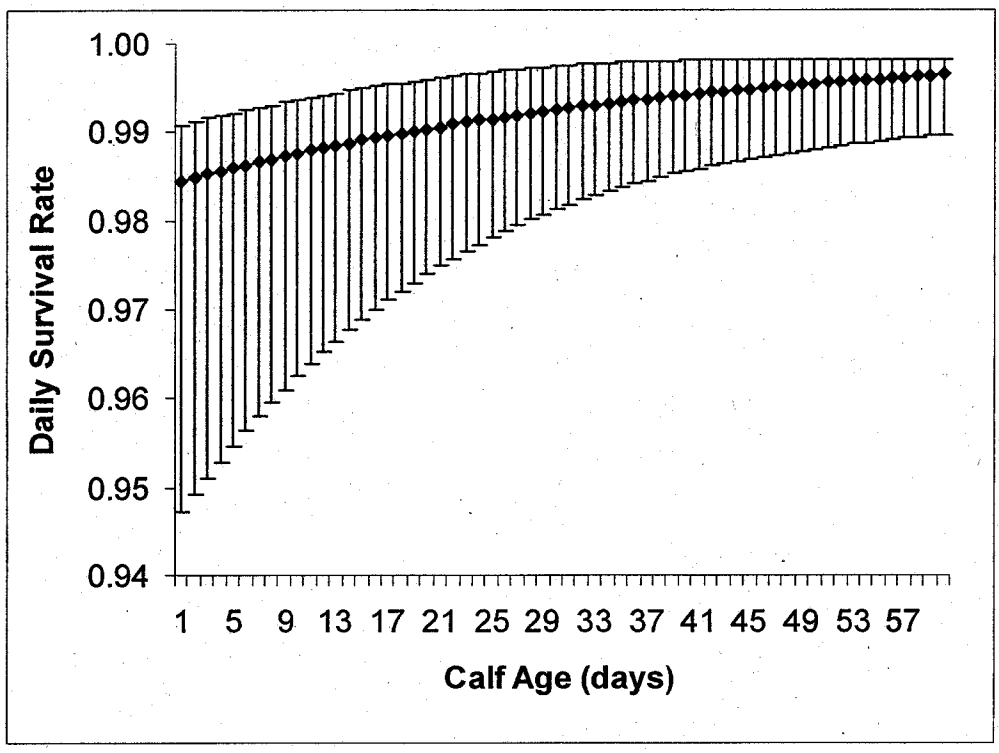


Figure 1-7. Estimates of daily survival rate (DSR) in nest-survival analysis of program MARK for unmarked calves in northern New Hampshire, 2002-2005. Pooled data from best-fitting model {S(age)} for calf age to 60 days and error bars represent 95% confidence intervals.

little support (ΔAIC_c=2.269 and AIC_c weight=0.188). Model S(birth date) received minimal support with a ΔAIC_c value >5 indicating little variation in survival over summer in relation to date of birth.

Discussion

Productivity

Excluding the July births of one cow, the calving period (8 May-11 June) occurred earlier and was 2 weeks longer than measured in Quebec (18 May-8 June, Laurian *et al.* 2000) and worldwide (19 May-8 June, Sigouin *et al.* 1997). Estimated median parturition dates (17-22 May) in this study were similar to estimates (18-20 May) documented by Addison *et al.* (1993) in central Ontario, but earlier than most reported in the interior of Alaska (20-27 May; Bowyer *et al.* 1998, Testa *et al.* 2000, Bertram and Vivion 2002). Synchrony of parturition was consistent with 80% of births occurring within 10-14 days each year as also observed in Alaska (80% in 11-17 days; Bowyer *et al.* 1998, Keech *et al.* 2000, Testa *et al.* 2000).

Timing and synchrony of birthing in moose is hypothesized to be adaptive to climatic patterns that provide optimal conditions to raise young (Bowyer *et al.* 1998, Keech *et al.* 2000). It is suggested that moose time parturition to maximum forage availability during summer (Bowyer *et al.* 1998, Keech *et al.* 2000), although little evidence exists of a proximal relationship between environmental conditions (i.e., snow depths and temperatures) and timing or synchrony of calving (Sigouin *et al.* 1997, Bowyer *et al.* 1998). Synchrony in caribou (*Rangifer tarandus*) populations was most related to plant phenology not predation (Post *et al.* 2003). Others propose that parturition is timed to avoid predation (Adams *et al.* 1995, Testa *et al.* 2000). If

predation influences timing of parturition in moose, increased calf survival should be observed for calves born during the peak of the birthing period (Bowyer *et al.* 1998, Keech *et al.* 2000). However, summer survivorship was not higher for calves born during peak parturition nor was survival dependent on birth date, although the lowest survival rate (0.55) occurred in 2005, the year with the least synchrony and later births. The relatively high calf survival (0.71) in the first two months suggests that predation probably does not limit or influence timing of calving in northern New Hampshire. The annual consistency of parturition dates most likely reflects the relationship of abundant forage resources and high energetic requirement associated with lactation and optimal growth rate of calves.

Reproductive status of yearling cows is an indicator of population condition, can be highly variable (Schwartz 1997), and was assessed previously in New Hampshire (Adams and Pekins 1995). The pregnancy rate (PSPB assay, 20%) and calving rate (direct observation, 30%) of yearlings were lower than the mean pregnancy rate (fetal count, rectal palpation, or direct observation) reported in North America (49%, Boer 1992), but similar to that measured in Michigan (10-30%, Dodge 2002). Yearling fecundity rates in moose populations above, near, and below carrying capacity were 18, 41, and 64%, respectively (Boer 1992); fecundity rate (calves/cow) in this study was 0.35.

Nutritional status and body size determines whether a yearling cow breeds and produces young (Saether and Haagenrud 1985, Schwartz and Hundertmark 1993) and ovulation rates provide indirect evidence of reproductive condition (Schwartz 1997). Yearling ovulation rates average 49% and range from 0-100% in North America; lower

reproductive rates indicate high ova loss (Boer 1992). Ova loss in adults averages 4.4% and was 9.3% in captive Alaskan adult moose (Schwartz and Hundertmark 1993, Scwhartz 1997). The yearling ovulation rate in 1999-2004 was 12% higher than the yearling calving rate (30%); the small sample size and ova loss could account for this difference. A similar reduction was also observed in yearling ovulation rates and fetal counts in New Brunswick (50 to 39%, Boer 1987), Newfoundland (60 to 46%, Pimlott 1959), and Montana 48 to 32%, Schladweiler and Stevens 1973).

The decline in ovulation rate and field-dressed weight of yearling cows since 1988-1998 in New Hampshire suggests a relative change in body condition. On poor habitat yearlings have low ovulation and pregnancy rates (Schwartz 1997) and adult cows should express similar declines as well, however, these parameters increased in adult cows during the same time period. Therefore, it seems unlikely that habitat quality was directly related to the yearling cow measurements. Of importance to productivity of local and regional populations is that the field-dressed weight of yearlings has declined to 204 kg statewide, and 210 kg in the study area; yearlings <200 kg are not reproductive (Adams and Pekins 1995).

Lower ovulation rates and productivity of yearling cows could be related to the impact of tick infestations endured as calves the previous winter. Addison *et al.* (1994) reported that captive moose calves heavily infested with winter ticks in fall had lower weight gain than moderately infested or uninfested calves. Captive, tick-infested moose with extensive hair loss had less visceral fat stores than animals with little hair loss (McLaughlin and Addison (1986). Yearling cows need to maintain high fat reserves for both successful pregnancy and winter survival (Heard *et al.* 1997). Ticks are not known

to cause anorexia in captive moose fed quality diets (Samuel 2004), but anorexia and weight loss were observed in cattle experimentally infested with the tick *B. microplus* (Seebeck *et al.* 1971).

Adult ungulates normally exhibit compensatory growth after nutritional stress of winter (Watkins *et al.* 1990), whereas young ungulates are unable to compensate under certain conditions (Schwartz *et al.* 1994, Schultz and Johnson 1995, Keech *et al.* 1999). Pimlott (1959) proposed that calf nutrition the first winter determines if puberty is reached the following breeding season. Female elk calves that experienced a harsh winter were less likely to breed as yearlings (Hancock 1957), and much of the variation in yearling pregnancy was attributed to previous winter severity (Houston 1982). Excessive winter weight loss in calves due to tick infestation may influence their breeding as yearlings because summer nutrition is allocated more to recovery than growth. For yearling cows, reproducing at a small body size likely imposes a larger risk on future fecundity as compared to adults (Sand 1996b). The decline in CL counts and calving rate of yearlings may be related to lower body condition and growth, although harvest weights suggest most yearlings are of adequate breeding weight. Annual monitoring of body weight and productivity of yearling cows is warranted given their declining trends, the importance of yearlings as an indicator of population status (Adams and Pekins 1995), and yearling productivity is key to maintain population stability and growth.

It has been reported that cows with greater rump fat had higher rates of pregnancy and twinning, and young with higher birth weight and survivorship, than cows with less rump fat (Keech *et al.* 2000). Adult pregnancy rate (78%) measured by blood assay and

ultrasound was slightly lower than the mean adult calving rate (85%). These rates were higher than the pregnancy rate measured in the Upper Peninsula of Michigan (74%, Dodge 2002) and lower than that measured in Ontario (97%, Bergerud and Snider 1988). While the annual adult calving rate varied from 77-92%, the mean was similar to that across North America (84%; Boer 1992; 74-100%, Gasaway *et al.* 1992) (Table 1-13). Even though the mean calving rate was relatively high and mean calf age was 2.0 d at first detection, the calving rate could have been slightly biased by neonatal mortality at <2 days.

The average twinning rate was 11% (range=9-20%) and fell within the range (5-25%) of a population near carrying capacity (Gasaway *et al.* 1992), although an average rate of 49% (range=4-90%) was cited for 25 North American populations (Franzmann and Schwartz 1985, Boer 1992, Gasaway *et al.* 1992, Heard *et al.* 1997). Although twinning may have been underestimated, the annual rate was similar among years and was primarily observed in cows (67%) that gave birth to twins in previous years. Variation in twinning has been associated with body condition of moose (Testa and Adams 1998, Keech *et al.* 2000), habitat quality, and population density (Franzmann and Schwartz 1985, Gasaway *et al.* 1992). Neither adult field-dressed weight or habitat quality within the study area was considered low or inferior.

Moose fertility, especially the probability of multiple ovulations, is related to both age and body weight (Saether and Haagenrud 1983, Adams and Pekins 1995, Sand 1996b). The annual ovulation rates of adults (91-93%) were at the high end of the range observed in North America (71-100%, Boer 1992). The average age of harvested adults was similar among time periods and within the age range of maximum productivity in

Table 1-13. Comparison of reproductive and survival estimates of cow moose in North America and Scandinavia.

Study area	Moose /km^2	Pregnancy rate %[a]	Twining rate %	Annual cow survival%	Main mortality source	Reference
New Hampshire	0.78	85[b]	11[b]	87	Vehicle collision/hunting	This study
UP, Michigan	0.28-0.29	74[c]	19[b]	88	Parasite/natural	Dodge 2002
NW Minnesota	-	48[c]	17	79	Parasite/disease/ starvation	Cox *et al.* 2006
Interior, Alaska	1.1	88[c]	21[b]	92	Brown bear/wolf	Keech *et al.* 2000
E Interior, Alaska	0.13-0.18	89[a]	63[b]	88	Wolf	Bertram and Vivion 2002
EC Alaska	0.13-0.19	100[d]	52[b]	91	Brown bear/wolf	Gasaway *et al.* 1992
SC Alaska	0.71	81[d]	38[b]	95	Brown bear	Ballard *et al.* 1991
SC Alaska	0.39-0.81	82[b]	17[b]	92	Wolf	Testa 2004
NW Territories	0.14-.0.16	86[b]	31[b]	85	Wolf	Stenhouse *et al.* 1995
SW Yukon	0.14	84[d]	28[b]	91	Brown bear	Larsen *et al.* 1989
NE Alberta	0.18	82[b]	33[b]	75	Hunting	Hauge and Keith 1981
Norway (2 areas)	-	77[b]	-	83-93	Hunting	Stubsjøen *et al* 2000

[a] Cows ≥2 yr at time of breeding.
Determined by direct observation[b], PSPB assay [c], and rectal palpation[d].

cow moose (4.0-7.0 yr; Sylven 1980, Saether and Haagenrud 1983, Schwartz and Hundertmark 1993). The field-dressed weight of cows ≥3.5 yr 1999-2004 averaged ≥274 kg statewide compared with 257 kg in 1988-2004; females in New Hampshire exceeding 275 kg typically have 2 CL (Adams and Pekins 1995).

While annual ovulation rates remained similar, the number of CL per animal declined between the periods of 1988-1998 and 1999-2004 despite an increase in mean weight of adults in each age class (Table 1-5). Testa and Adams (1998) found a relationship between fall body condition of cows and pregnancy but not between condition and ovulation or twinning; multiple ovulations were lower than the rates of twins in other Alaskan populations (Boer 1992, Gasaway *et al.* 1992). Their results suggest that low potential for twins could reflect nutritional or genetic constraints (Testa and Adams 1998, Testa 2004). Of the 9 sets of twins observed in this study, 3 adult cows were known to twin in multiple years (6 sets). In Sweden, Sand (1996a, 1998) reported a positive correlation between multiple ovulations (probable twinning) by moose in successive years indicating that twinning in moose may be a phenotypic trait. Ovulation rate in Sweden was positively related to the number of calves produced during the current year, and not attributed to variation of age and carcass mass; although body growth was affected by lactation costs, future fecundity (multiple ovulation) was not. Cows that reared twins into fall weighed 7% less than other cows in the same reproductive category (Sand 1998). In both the study area statewide, field-dressed weights of adult cows increased 5-13% within the 3.5, 4.5, 5.5, and ≥6.5 yr old age classes between 1988-1998 and 1999-2004, whereas multiple ovulations declined.

Adult twinning rate is highly correlated with yearling pregnancy rate signifying

that each may be influenced by similar factors (Boer 1992). Variation in reproductive strategies may be an adaptive response to the environment and stress (Sand 1996b, 1998). In Sweden, cows that experienced more severe climatic conditions had to attain 22% higher body mass to achieve the same probability of multiple ovulations compared to cows in less harsh environments (Sand 1996b). Winter tick infestations that reduce overall condition may also influence fecundity of adults as reflected in reduced CL counts and twinning rate. Larger body size should be an advantage to compensate for the negative influence of tick infestations on gestation and lactation.

Another possible explanation for the low twinning rate and the decline of multiple ovulations and yearling fecundity is higher population density. Both twinning rate and calving rate of yearlings were comparable to a population near carrying capacity. Various studies have reported density dependence effects on adult fecundity and increasing age of first reproduction of ungulates (Kie and White 1985, Clutton-Brock *et al.* 1987, Festa-Bianchet *et al.* 1995, Stewart *et al.* 2005), although density-dependence effects are generally less evident in adult fecundity (Gaillard *et al.* 2000). In red deer (*Cervus elaphus*) an increasing body mass threshold for fecundity occurred at higher densities and was an adaptive strategy to increase calf survival and reduce risk of late winter mortality of cows (Albon *et al.* 1983). However, the twinning rate of moose in Scandinavia did not decline with increasing density and no density-dependent decline in body weight was detected (Sand 1998, Solberg *et al.* 1999). The reasons for low twinning rates and decline in number of CL per adult cow in northern New Hampshire are uncertain, however, decline in habitat quality does not seem implicated because field-dressed weights, reproductive data, and survival of adults were not representative of a

habitat-limited population.

Cause-specific Mortality of Radio-marked Moose

Winterkill/parasite Mortality

Mortality of most individuals was attributed to winterkill/parasite because snow conditions throughout the study were not considered severe or the direct cause of mortality. Excessive snow depth in Alaska has been linked to high calf mortality (Franzmann 2000); 70 cm of snow impedes moose mobility, and 90 cm is indicative of severe conditions that confine movement and increase mortality (Coady 1974). A monthly maximum snow depth of 90 cm was exceeded only once, but did not persist and was recorded in 2005 when no adult winter mortality occurred, however, no calves were radio-marked. The only winter mortality of cows >1.5 years old (n=3) occurred in 2002 when the maximum snow depth recorded was <36 cm, and the mean ambient temperature in January-March (-3.7°C) was above normal and the highest recorded in any year of the study.

Calves and adult cows categorized as winterkill/parasite had mean %FMF of 16.5% and 11.6%, respectively, and were classified as poor body fat and poor condition. Femur fat content <10.0% in calves and <20.0% in adults is representative of moose starving or approaching starvation (Franzmann and Arneson 1976, Peterson *et al.* 1984). Given adequate habitat and lack of winter severity, poor body condition and winter nutritional stress were undoubtedly related to the influence of winter ticks. All calf mortalities had measurable winter tick infestations and many were infested with lungworms (Table 1-9).

Mortality factors rarely act alone to influence animal populations and the impact

of parasitism is heightened when an animal is nutritionally stressed (Lankester and Samuel 1997). Certain data suggest that smaller cows and calves may be more susceptible to winterkill/parasite. None of the 4 cow mortalities in 2002 were pregnant, and of 11 calves monitored since birth and later collared, 2 of 3 that died were born after 11 June, nearly a month past peak parturition. Late-born calves are often unable to attain optimal body condition prior to winter (Clutton-Brock *et al.* 1982), and cows with higher rump fat have high rates of pregnancy and heavier calves (Keech *et al.* 2000). Although birth date did not influence summer survival of calves, it may influence winter survival and long-term life history traits.

There are numerous accounts of late winter mortality of tick-infested moose with extensive hair loss. Earliest reports were in the early 1900's in New England, Minnesota, Nova Scotia, and western Canada (Samuel 2004). Substantial die-offs in conjunction with heavy tick infestations have been reported throughout North America including Alberta (Samuel and Barker 1979), Minnesota (Lenarz 1992), Algonquin Provincial Park in Ontario (Garner and Wilton 1993), and most recently, widespread in Canada in 1998-1999 (Samuel 2004), and throughout western Canada, Maine, Vermont, New Hampshire, and Isle Royale in 2001-2002 (Samuel and Crichton 2003).

The relationship between moose and winter tick appears to be relatively recent in evolutionary terms, consequently, moose may not have developed an optimal grooming response to ticks in comparison to efficient groomers such as white-tailed deer and elk that also carry winter ticks (Anderson and Lankester 1974, Samuel 2004). Therefore moose presumably carry a high density of winter ticks and suffer greater consequences than other ungulate hosts (Samuel 2004). Moose average about 35,000 ticks and

commonly have >50,000, and in rare cases may have >80,000 ticks (Mooring and Samuel 1988, Welch and Samuel 1989, Welch *et al.* 1991, Samuel 2004). In comparison, elk and deer average 1,200 and 540 ticks (less than one-tenth as many) proportional to body size (Mooring and Samuel 1998). Moose calves infested with approximately 30,000 ticks lose about 8 liters of blood (58% blood volume) to engorging adult females in March-April; adult cows lose about 3.2 liters (11%) due to differences in tick age and sex composition. Interestingly, calves average approximately 25.6% female ticks and cows only 18.0%; this discrepancy is unexplained but may be due to lack of resistance or grooming by calves as compared to adults which are infested repeatedly each year (Samuel 2004). Because moose, and particularly calves, are in negative energy balance in late winter (Schwartz and Renecker 1997), the energetic cost associated with compensating for blood loss further exacerbates their steadily declining condition (Lankester and Samuel 1997, Samuel 2004). Although cows in the last trimester are at risk, prime bulls suffering from high energy expenditure and decreased foraging during the rut may be as vulnerable to mortality as calves.

Grooming relieves irritation from feeding ticks, but also reduces time spent feeding and resting (Mooring and Samuel 1999) and increases damaged or hairless areas that result in greater heat (energy) loss in winter (McLaughlin and Addison 1986). Hair loss on captive moose was positively correlated with the total number of adult ticks; minimal hair loss was observed in October-January with rapid loss in February-April, and severe alopecia was linked to lower visceral fat deposits and reduced weight gain in calves (McLaughlin and Addison 1986). Captive calves that were heavily tick-infested gained less weight in fall than uninfested or moderately infested calves (Addison *et al.*

1994). Hypothermia probably has minor influence on moose mortality because hair loss is greatest in March-April at the end of winter (Welch *et al.* 1990, Samuel 2004), however, hair loss can contribute to the negative energy balance of calves through heat loss and reduction in body fat (McLaughlin and Addison 1986). Although weather is normally less severe at this time, unusually wet and cold temperatures undoubtedly impact thermoregulation of calves in April.

Weather and environmental conditions influence seasonal and annual winter tick populations (Drew and Samuel 1986, Samuel and Welch 1991, Wilton and Garner 1993, Samuel 2004). Warm temperatures and snowless conditions during fall presumably increase success of questing tick larvae. Questing ceases at <0°C or when ticks are buried by snow, although larvae can survive in aggregations well past November (Samuel and Welch 1991). Conversely, snow cover and low temperature reduces survival of engorged female ticks dropping from moose in April (Drew and Samuel 1989, Samuel and Welch 1991, Samuel 2004); temperatures below 3-4°C are detrimental to tick survival (Wilton and Garner 1993).

In each April the mean ambient temperature was >4°C, and other than 15 cm of snow cover in mid-April 2001, only trace snow occurred, conditions conducive for high survival of adult female ticks. In all years mean ambient temperature was >0°C in September-November and <0°C in December, and initial snowfall and snow cover occurred in November, normal conditions in northern New Hampshire. However, in November 2001 snow depth was <1 cm and the mean ambient temperature in December (–1.1°C) was >5° above normal; no snow was present in mid-December when aggregations of tick larvae were commonly observed during captures. These specific

conditions may have been optimal for prolonged questing and high transmission rates of larvae onto moose. Annual tick density and moose mortality increased with moose abundance in a population with no predators in Alberta, Canada (Blyth 1995). Therefore, controlling moose numbers through harvest may be the best way to manage tick populations (Samuel 2004). Although tick transmission could increase where moose abundance is greater, weather patterns probably have more influence on overall tick density. DelGiudice *et al.* (1997) reported tick-related nutritional stress in moose and that effects of ticks were primarily weather-dependent and density-independent. Density may be more important for a growing population, but other factors appear more important for a population at or near carrying capacity (Lankester and Samuel 1997).

Most mortality (calves and adults) in winter 2002 was attributed to winterkill/parasite, whereas, calf survival was higher and no adult mortality occurred in winters 2003-2004. Hair loss and damage was also more severe in 2002 than in 2003-2004. A high incidence of dead, tick-infested moose was noted throughout northern New England, Michigan, and Canada the same year (Samuel and Crichton 2003). Mortality associated with winter ticks combined with other factors (e.g., lungworm) is probably an annual event for moose calves, however, elevated calf mortality and some mortality of yearlings and adults should be expected in years of tick epizootics. Although April conditions are important in the tick life cycle, unseasonably warm and snowless conditions in November and December probably best forecast potential tick epizootics and abnormal winter mortality of moose. Long-term climatic fluctuations causing extended periods of warm weather and shorter winters may prove detrimental to moose populations in New England if tick-related mortality continually reduces productivity and

survival. The most important dynamic of winter ticks for moose managers is the frequency of epizootics.

In 2003-2004, 9 of 10 calves had infestations of lungworm with varying degrees of tick-related hair loss. Although specimens were never identified as *D. viviparous*, their identity was assumed because of their wide distribution and they are common in Maine moose (Lankester and Samuel 1997, Morris, Maine IF&W, pers. comm.). Lungworm was not identified in 2002 field necropsies, but identification was problematic that winter. Elk in poor condition due to heavy tick burden or inadequate nutrition are more susceptible to winter mortality when infested with lungworms (Worley 1979, Thorne *et al.* 2002). Additionally, dead black-tailed deer (*Odocoileus hemionus columbianus*) fawns exhibiting hair loss were infested with biting lice (*Tricholipeurus parallelus*) and *D. viviparous* (Bender and Hall 2004). Although controlled research is limited, calf mortalities in Maine had infestations of *D. viviparous* and winter ticks in late winter 1995 (Morris, pers. comm.). While this parasite is probably not the primary cause of death, combined infestations of lungworms and winter ticks are more detrimental than singular infestations. No evidence was found of brainworm (*Parelaphostrongylus tenuis*) or large American liver fluke (*Fasciolides magna*) in radio-marked animals suggesting that neither are a significant mortality factor in the study area. However, examinations for brainworm were limited to searches within the brain cavity.

Three of the total undetermined yearling and adult mortalities (n=4) occurred in 2002 with two deaths likely influenced by winter tick infestations, but carcasses showed symptoms that were less severe than mortalities characterized as winterkill/parasite. Since the mid-1980's, a mysterious wasting disease has been the source of moose (*Alces*

alces L.) mortality in southwestern Sweden (Broman *et al.* 2002). Although the exact cause is uncertain, animals exhibited nontraumatic symptoms such as anorexia, emaciation, weakness, lack of human fear, and circling. Several plausible hypotheses have been formed involving food-related and host-parasite (viruses, bacteria, fungi, or protozoa) causes (Broman *et al.* 2002). While wasting disease cannot be ruled out for the undetermined cases in this study, mortality was limited compared to frequency observed in Sweden.

Human-related Mortality

Vehicle-related mortalities were concentrated in May-June (50%) and 60% were at roadside salt licks. Approximately 240 moose-vehicle mortalities are reported annually in New Hampshire as compared to about 600 in Maine; annual averages of 78 and 76 mortalities (2001-2003) were observed in the North and White Mountain management regions, respectively (Bontaites 2004). A vehicle-collision annual mortality rate of 0.04 was observed in Alaska where it was the main mortality of for radio-marked adult cows (Bangs *et al.* 1989). The average annual rate of 0.06 in this study applied to the estimated moose abundance (n=1500) in the study area predicts 90 deaths, a reasonable estimate relative to the 3-year average of 78. Although this was the second leading cause of death for study moose, annual vehicle-collisions appear to be stable and related to seasonal use of roadside salt licks.

Roadside salt licks are considered a major cause of increased moose-vehicle collisions during June-July in Quebec, Ontario, and New Hampshire (Jolicoeur and Crête 1994), whereas, salt lick use was the probable cause for increased collisions between June-September in Minnesota (Belant 1995). Sodium and mineral content in roadside

salt licks are higher than in surrounding streams and puddles, enabling moose to obtain sodium more efficiently in licks than by foraging aquatic plants (Miller and Litvaitis 1992). Moose in northern New Hampshire most actively use licks during low-light conditions between 2000-0600 hr (Silverberg *et al.* 2002), and 80% of study moose were known to use roadside salt licks and some traveled up to 15 km. Moose-related collisions in northern New Hampshire will most likely remain a problem due to the repeated use of road salt as a deicer, inadequate roadside drainage, continued moose accessibility to preferred licks, and summer traffic associated with increased tourism and outdoor recreation.

Hunting can be a substantial form of mortality and often exceeds natural mortality rates of calves and adults as in Norway (Stubsjøen *et al.* 2000). Hunting was the leading form of mortality for adult cows (n=5); calves were radio-marked post-hunt and therefore absent from mortality, however, calves represent <5% of the harvest within the study area (Bontaites 2004). Hunter harvest is easily influenced by management decisions regarding hunting regulations, hunter distribution, and hunter access (Modafferi and Becker 1997). The WMUs in the study area averaged 115 either sex permits with >85% harvest success during the study; bulls, cows, and calves accounted for 83, 15, and 2% of the 2004 harvest (NHFG 2004). Excluding areas within the White Mountain National Forest, hunter access was excellent due to numerous open logging roads which probably increased hunter success. The 7 study animals harvested were all in close proximity to logging roads and within current or recent logging activity.

Harvest rates of 2-17% are reported for moose populations throughout North America, but are as high as 25% in Quebec where low natural mortality occurs (Crête

1987). If population growth is the objective, harvest rates generally are <10-12% (Timmerman and Buss 1997). On average 390 animals are harvested in New Hampshire annually from an estimated population of 5,000-6,000 moose for a harvest rate of 7-8%; about 7% (n=1500) in the study area including 1% cows was harvested in 2004 (Bontaites 2004, NHFG 2004). Although the estimated mortality rate (0.04) for marked cows was slightly higher than that in the region, it is normally thought to be biased due to hunter preference for unmarked animals. High hunter selectivity was suspected in Norway because no marked cows were taken despite a cow harvest rate of 13.8% (Stubsjøen *et al.* 2000). However, the overall conservative cow harvest has negligible effect on productivity in the study area.

Although problematic to quantify, illegal kill (poaching) appears low with a 5-year statewide estimate of 3 animals, however it is a minimum estimate (Bontaites 2004). Poaching has been estimated as low as 5-10% and as high as 100% of the legal harvest in a review of the socioeconomic impact of moose in North America (Wolfe 1987). Moose in the study area were vulnerable to poaching because of the remoteness and unlimited access to prime moose habitat through an extensive maze of logging roads. Despite this, poaching in the study area is most likely limited and may primarily occur during the annual moose hunt when concealment is less difficult (Conservation Officer Wayne Saunders, NHFG, pers. comm.). Only one of 92 animals was unaccounted for at termination of the study, and none were illegally killed. However, marked cows would probably not be perceived as an optimal poaching target.

Vehicle collisions and hunting represented 69% of yearling and adult radio-marked cow mortality (n=16). Although these human-related causes were the highest

source of mortality in a potentially biased sample, their effect is minor because annual cow survival is high (0.87). Summer vehicle collisions and fall harvest were basically stable each year, and measurable late winter mortality occurred only in 2002. Likewise, the survival analysis indicated that yearling and adult survival were more dependent on year not season. Therefore, under the current harvest strategy, survival of cows may be most influenced by natural mortality factors, notably annual fluctuations in winter tick, however, hunter harvest represents the primary mechanism to influence productivity and abundance.

Survival Analysis

Radio-marked Cows

Annual survival rate (0.74-0.91) and overall cow survival (0.87) were similar to those in hunted populations with little to no predation in Norway (0.83-0.93, Stubsjøen *et al.* 2000) and an unhunted population in the Upper Peninsula of Michigan (0.88, Dodge 2002), and higher than those in a parasite-affected (liver fluke and brainworm) population in Minnesota (0.79, Cox *et al.* 2006). Survival rates in Alaska and Northwest Canada were more varied (range=0.75-0.95, Table 1-13).

The variation in weekly survival between years (2002-2004) was due to late winter mortality from winterkill/parasite and undetermined cases in April 2002. The only late winter adult mortality occurred in 2002, suggesting that tick epizootics can influence survival rate of cows. Adult female survival of large herbivores appears to be normally buffered against temporal variation and always less variable than juvenile survival, although epizootics have caused substantial differences in annual survival of adults (Cransac *et al.* 1997, Gaillard *et al.* 1998). Excluding early winter when no mortality

occurred, survival was similar among seasons. Summer (0.96) and winter survival (0.96) were consistently high and similar to that in Michigan (0.95 and 0.91, Dodge 2002) and Norway (0.99 and 0.98, Stubsjøen *et al.* 2000). Fall survival (0.94) was higher than in an intensely harvested (0.85) population and lower than in a population with limited adult harvest (0.96) in Norway (Stubsjøen *et al.* 2000). The high survival of adult cows in New Hampshire can be attributed to lack of predation, a conservative cow harvest, moderate winter conditions, and good body condition in fall.

Radio-marked Calves (~7-12 months of age)

Winter survival rate of calves from ~7-12 months of age (0.67) was lower than that in populations with little to no predation in Michigan (0.84, Dodge 2002), Norway (0.83-0.98, Stubsjøen *et al.* 2000), and Sweden (~0.89, Ericsson *et al.* 2001) (Table 1-14). In Alaska, high winter calf mortality was observed in winters with severe weather conditions (Ballard *et al.* 1991, Franzmann 2000, Testa 2004), and where summer predation was low, winter mortality of calves was even higher (Ballard and Van Ballenberghe 1997). Most Alaskan populations experience higher winter survival than summer survival; >85% calf survival occurred after the first month of life in a high-density moose population (Keech *et al.* 2000). Winter calf survival in Alaska ranges from 0.77-0.94 (Table 1-14). Contrary to Alaska, calves in our study were not influenced by winter predation or winter severity (but winters were mild), instead, mortality was attributed to parasite infestations and related malnutrition. There was a consistent trend of among- and within-winter variation of calf survival; survival was high in early winter in comparison to late winter when mortality risk increased and 88% of winter mortality occurred. Survival in 2002 was lower than in 2003-2004 but no variation in weekly

survival was detected between years; precision of weekly survival estimate was likely influenced by collar loss (small sample size) in 2002. Documentation of substantial tick-related mortality of radio-marked moose calves was unique to this study. When epizootics occur, ticks can dramatically reduce calf survival and recruitment and in combination with severe winter weather, could probably cause >50% calf mortality.

Unmarked-calves (0-2 months of age)

Despite summer survival ranging from 0.55-0.81, overall survival rate the first 60 days (0.71) was higher than in most Alaskan populations experiencing substantial predation, yet lower than in populations unregulated by predation (range=0.24-0.86, Table 1-14). High survival was observed where predation was limited in Sweden (~0.87, Ericsson *et al.* 2001). In a review of northern temperate ungulates, mean survival of neonates was 0.53 where predators occurred and 0.81 in predator-free populations (Linnell *et al.* 1995). Neonatal survival in New Hampshire was probably slightly overestimated because some mortality most likely occurs prior to the initial observation of a calf. However, bias was probably minimal because the mean estimated calf age at first detection was 2.1 d and the adult calving rate was 85%.

Most calf mortality occurs within the first 6 weeks of life (Ballard and Van Ballenberghe 1997) and 84% was observed in this study during that period. Predation is the main source of neonatal mortality in moose calves, although accidents such as drowning can account for 15% of deaths (Gasaway *et al.* 1992). Black bears are a principle predator of moose calves and radio-telemetry studies have revealed that they kill high numbers of calves (Franzmann *et al.* 1980, Osborne *et al.* 1991, Ballard 1992, Bertram and Vivion 2002). Neonates were not marked and cause of death was unknown,

Table 1-14. Comparison of moose calf survival estimates from North America and Scandinavia.

Study Area	Moose /km^2	Survival %				Main mortality source	Reference
		8 week	~0-6 months	Winter (~7-12 months)	Annual		
New Hampshire	0.78	71	-	67	~45	Winterkill/ parasite	This study
UP, Michigan	0.28-0.29	-	84	84	71	-	Dodge 2002
NW Minnesota	-	-	-	-	66	-	Cox *et al.* 2006
Interior, Alaska	1.1	~75	-	-	53	Bear/wolf	Keech *et al.* 2000
E Interior, Alaska	0.13-0.18	39	-	94	20	Black bear	Bertram and Vivion 2002
EC Alaska	0.13-0.19	24	21-24	85-88	18-21	Brown bear	Gasaway *et al.* 1992
W Interior, Alaska	0.21	49	-	-	32	Black bear	Osbourne *et al.* 1991
SC Alaska	0.71-0.84	-	~39	88	33	Brown bear	Ballard *et al.* 1991
SC Alaska	0.39-0.81	33	26	78	20	-	Testa 2004
NW Territories	0.14-0.16	86	65	-	44	-	Stenhouse *et al.* 1995
SW Yukon	0.14	40	32	77	25	Brown bear	Larsen *et al.* 1989
NE Alberta	0.18	~61	-	-	27	-	Hauge and Keith 1981
C Alberta	0.64	-	73	-	67	-	Mytton and Keith 1981
Norway (2 areas)	-	-	69-87	83-97	66-70	Hunting	Stubsjøen *et al* 2000
Sweden	0.70-0.90	~87	~53	~89	48	Hunting	Ericsson *et al.* 2001

but similar timing (76% in first 28 days of life) of most mortality each year suggests that the cause was consistent. Predation was expected because black bears account for substantial calf mortality where they outnumber other large predators and their density exceeds 0.20/km^2 (Ballard 1992); bear density in the study area was estimated at 0.23-0.34 bear/km^2 (Timmins, bear project leader NHFG, pers. comm.). There were several eyewitness accounts of bear predation of non-study calves in the study area and bears were routinely observed while performing walk-ins. On occasion bears were in close proximity to cow-calf pairs although no direct evidence of predatory stalking was observed. Another possible predator was the coyote which was responsible for <1% of calf mortality in Alaska (Ballard *et al.* 1991). Limited moose remains have been found in coyote scat in Maine and Quebec but it is unclear whether it was scavenging or predation (Litvaitis and Harrison 1989, Samson and Crête 1997).

In regions of high predator numbers such as Alaska, predation can account for 95% of mortality, 45% due to black bears (Bertram and Vivion 2002). Bear kill rates are independent of moose population density (Ballard and Van Ballenberghe 1997), however, these data were based primarily on several studies in three areas of Alaska (Ballard and Van Ballenberghe 1998). Due to small sample sizes, little is understood about the impacts of black bear predation on moose populations (Ballard and Van Ballenberghe 1998).

Most black bear predation on moose calves occurs within 30 days of birth (Schwartz and Franzmann 1991) and generally ceases by 1 July when calves >1 month old seem capable of escaping bears (Franzmann *et al.* 1980, Franzmann and Schwartz 1986); in this study ≥76% of calf mortality occurred in the first month. Additionally, 4

cows lost a calf in more than one summer (44% of summer mortality) with 2 cows losing calves in 3 summers. Some mortality could be related to lack of maturation and attentiveness of various cows because maternal experience in white-tailed deer reduced vulnerability to predation (Ozoga and Verme 1986).

Models suggested that age-specific survival increased as calves aged (0-60 days), similar to results of Testa *et al.* (2000) who found that age-specific, daily mortality rate of calves declined in a linear trend from 0.04 to 0.0/day at 65 days of age. Survival of calves in this study was not higher for calves born during peak parturition (15-21 May; 51% of births occurred) and the models also suggested that survival was not dependent on date of birth. Several studies have demonstrated that calf survival was not influenced by timing and synchrony of births (Bowyer *at al.* 1998, Keech *et al.* 2000), whereas, other research suggests poor summer survival of early and/or late-born calves (Adams *et al.* 1995, Testa *et al.* 2000). The relatively high summer survival of calves in this study suggests that predation and incidental mortality are moderate in northern New Hampshire, and that summer mortality of calves is probably not a limiting factor of population abundance in the study area.

Annual Calf Survival

Unmarked calves were not monitored as frequently post-summer as during the calving season, therefore, an estimated date of mortality was difficult to establish. However, positive identification of calf fate was made before the next calving season (n=30) and at least 2 of the 6 losses occurred in August-December (survival rate=0.93). Calf survival at ~3-6 months of age was also high (0.90) in areas of Alaska with little to no calf harvest (Keech *et al.* 2000, Bertram and Vivion 2002, Testa 2004), therefore,

survival during this time period was conservatively estimated at 0.95. The survival rates of unmarked calves at 0-2 months of age (0.71), and ~3-6 months (0.95), and survival of marked calves at ~7-12 months (0.67) were used to calculate an annual survival rate of 0.45 (i.e., 0.71*0.95*0.67 = 0.45).

In Michigan, annual calf survival was 0.71 (Dodge 2002) and in areas of Scandinavia with few to no predators, annual survival was high excluding deaths during the hunting season (~0.75; Stubsjøen *et al.* 2000, Ericsson *et al.* 2001). Annual calf survival in predator-rich environments of Alaska ranges from 0.18-0.33, whereas, areas with lower predation have survival rates >0.44 (Table 1-14). Juvenile survival and recruitment are highly sensitive to limiting factors regardless of whether variation is related to population density or stochastic environmental factors (Gaillard *et al.* 1998). Survival in the study area was lower than in populations with little predation and appears related to winter mortality (winterkill/parasite) associated primarily with winter ticks absent in many populations.

Management Implications

This study yielded important, undocumented, and novel information concerning population dynamics of moose in northern New Hampshire. Age-specific fecundity, survival rates, and mortality factors assist managers in assessing population status, and the data indicate that reproduction, productivity, and survival of adult cows were high, however, yearling fecundity and calf survival were relatively low. A tick epizootic in 2002 specifically reduced winter survival of adults and caused high calf mortality. Therefore, winter ticks, not habitat quality, had the most influence on population dynamics, through reduced calf survival, juvenile recruitment, and fertility. The impact

of winter ticks in the study was likely low on a relative scale because winter conditions were moderate-mild. Higher mortality rates should be expected in average-severe winters during a tick epizootic and ultimately tick-related mortality may be due to a combination of factors (e.g., lungworm, severe weather). The frequency of tick epizootics is likely the most important factor for moose managers.

Continuous reduction in survival and productivity of yearlings and calves can negatively influence population growth and stability of regional populations. Further understanding the annual and long-term role and influence of the winter tick on moose populations is warranted not only regionally but also statewide. Monitoring winter tick epizootics, fall and spring weather, degree of winter mortality, field-dressed harvest weights, and age-specific ovulation rate would provide a basis for understanding the relationships among these factors. Integrating these relationships into population dynamics models and harvest rates and quotas should be a priority of moose management in New Hampshire.

CHAPTER II

POPULATION MODELING

Introduction

Effective management of moose populations requires the ongoing assessment of a number of parameters that indicate or estimate their size, composition, growth rate, and productivity (Timmermann and Buss 1997). Wildlife managers routinely use population models as a mathematical tool to assess the dynamics of hunted populations and to predict the outcomes of harvest management programs (Pojar 1981, White 2000). Population models can be described as a bookkeeping system used to monitor demographic processes such as natality, mortality, age of first breeding, immigration, and emigration; these models can be used to predict population trends over time and to assess the influence of vital rates on population change (White 2000). Although a model may not include all population parameters to function, it must be based on reliable data with functional relationships to be useful (Kovach *et al.* 1998).

For many species, particularly ungulates, age is the most important determinant in the life history of an individual (Akcakaya *et al.* 1999, Gaillard et al. 2000). Age-structured models group individuals in a population by incorporating age-specific vital rates of surviving to the next age class and fecundity (Akcakaya 2000). The assumption is that demographic characteristics of individuals are related to their age and that there is little variation among individuals of the same age (Akcakaya 2000). Therefore, age-

structured models should help indicate how age-specific parameters affect the dynamics of population size and structure.

Abundance indices suggest that the moose population within the study area has approached stability despite perceived optimal habitat, minimal predation, and a conservative harvest (Bontaites 2004, pers. comm.). The primary objective of this exercise was to use age-specific fecundity and survival parameters of marked moose, with annual reproductive data of harvested moose, and abundance estimates from surveys to model moose population response. This exercise will assist managers to better understand and predict moose population dynamics and demographic parameters related to population stability in northern New Hampshire.

Methods

Model Structure

Age and stage-structured matrix population models were constructed with RAMAS (Ecolab v. 2.0, Setauket, New York; Akcakaya *et al.* 1999) to evaluate and predict temporal change in the moose population with data collected in December 2001-September 2005. In RAMAS Age and Stage, individuals are grouped by age class, and survival and fecundity rates per age class are used to construct a Leslie matrix (Akcakaya *et al.* 1999). The Leslie matrix model uses demographic rates to assess population trend over time (Leslie 1945). Moose were classified into 3 age classes: calves were ~7 months-1 yr, yearlings were $\geq$1 yr but <2 yr, and adults were $\geq$2 yr. Finite rate of increase (λ, lambda) and population size in 2015 were calculated. The exponential option was used, therefore, density dependence was not incorporated in the models providing a conservative assessment of population growth because of small population size

(Ginzburg *et al.* 1990). Immigration and emigration were not considered, but demographic stochasticity (natural changes in births and deaths) was incorporated by sampling number of survivors using binomial distribution and offspring from a Poisson distribution (Akcakaya 1991). The finite rate of increase is the dominant eigenvalue of the stage matrix and gives the proportional increase in total abundance under stable distribution which ignores density dependence, stochasticity, or dispersal (Akcakaya *et al.* 1999). Sensitivity and elasticity analyses were conducted on each age class (Akcakaya *et al.* 1999). Sensitivity analysis and its proportional equivalent, elasticity analysis, are a measure of each demographic vital rate's contribution to λ with the largest value having the most influence (Caswell 2001). Sensitivity analysis quantifies the effect on population growth of a fixed infinitesimal change in a vital rate, whereas elasticity analysis considers the influence of an infinitesimal change that is proportional to the average value of a vital rate (Zuidema and Franco 2001). All models were based on 1000 replications and projected for 10 years. Only the female population was modeled because bulls represented only a small percentage of the yearling and adult radio-marked population and their calf mortality and collar drops were high. Winter, summer, fall, and annual survival estimates of yearlings and adults combined were generated from weekly models in program MARK. Survival rates of winter-marked and summer-unmarked calves were calculated separately from weekly and daily survival rates in MARK (Table 2-1, see Chapter I).

When using life table data in a Leslie matrix, the timing of the census (establishes abundances) in relation to mortality, reproduction, and age definition determines how vital rate formulas are constructed for each age class (Akcakaya *et al.* 1999). Two post

Table 2-1. Model parameters used to construct Leslie matrices and estimate population growth rate of cow moose in northern New Hampshire, 2002-2005.

Parameter		Calf ($_c$)	Yearling ($_y$)	Adult ($_a$)
Survival (S)[a]				
	Winter ($_w$)[b]	0.668	0.963	0.963
	Winter lower 95% CI	0.529	0.906	0.906
	Summer ($_s$)	0.710	0.957	0.957
	Fall ($_f$)	-	0.940	0.940
	Fall lower 95% CI	-	0.864	0.864
Fecundity (F)[c]				
	Calves/Cow (M)	-	0.350	0.942
	CL/Cow (C)	-	0.421	1.240

[a] Survival estimates derived from analysis in program MARK.
[b] Combined early and late winter seasons.
[c] Fecundity estimates generated from walk-in observations (M) and corpora lutea counts (C) from 1999-2004 harvest data.

breeding models (census occurs after breeding) were developed to analyze the influence of two separate forms of fecundity. Model I incorporated walk-in data of calves with marked cows; Model II used ovulation rates of harvested cows in 1999-2004 from WMUs B, C1, and C2 in the study area.

Fecundity is described as the mean number of daughters per cow in each age class surviving to the next breeding season (Akcakaya *et al.* 1999). Model I used annual reproductive data of yearlings and adults from observations of marked moose in 2002-2005 (Fig. 2-1; see Chapter II). The fecundity estimate per age class (x) was calculated as, $F_x=MR\,S_{sc}S_w$ where:

F=fecundity of yearlings (F_y) or adults (F_a),
M=maternity, mean # of calves per yearling or adult cow from direct observation
S_{sc}=summer calf survival
R=female offspring ratio (0.50), and
S_w=winter yearling or adult survival.

Model II incorporated corpora lutea counts from reproductive tracts of yearling and adult cows harvested in WMUs B, C1, and C2 in 1999-2004 (Fig 2-1). Fecundity was calculated as, $F_x=CORS_{sc}S_w$ where:

C=mean corpora lutea count per yearling or adult cow,
O=mean ova success (0.956),
R=female offspring ratio (0.50),
S_{sc}=summer calf survival, and
S_w=winter yearling or adult survival.

The reproductive rates were assigned because mean ova loss of adult cows was 4.4% (Schwartz and Hundertmark 1993). It was assumed that calf fecundity was zero in all models. Although skewed sex ratio in calves has been reported, it is 50% normally (Schwartz and Hundertmark 1993).

In both models the lower 95% confidence intervals from winter survival rates of

calves and yearling/adults were used to simulate increased winter mortality from severe winter tick infestations or other winter-related sources (Table 2-1). Keeping other seasonal survival rates and fecundity rates constant, lower winter survival rate was changed in the matrix formula of each model independently for calves, and then for both calves and yearling/adults. A second simulation was run in both models using the lower 95% confidence interval of the fall rate yearling/adults to simulate potentially higher mortality related to poaching or unreported kills during the hunting season. Total abundance (n=1500) was estimated from moose observation rates by deer hunters during November surveys in WMUs B, C1, and C2 (Bontaites, pers. comm.). The average (2001-2004) observation rate of calves was 15% of total moose observed, and the average adult bull to adult cow ratio was 48:52; yearling and adult cows were not distinguished in the data (Bontaites, pers. comm.). The two models were evaluated with 3 different initial abundances of percent calves in the population; 15, 20, and 25% calves were considered (half female) because it was assumed that deer hunters commonly misclassified calves as yearlings or adults. Yearling abundance was calculated as the product of female calf abundance and survival (0.628, seasonal rate from MARK analysis) of calves from their first fall to the next. Adult abundance was calculated as 1500 minus 2X the sum of calf and yearling abundances (accounts for both sexes); adult cows were then calculated as 52% of the adult population, therefore, total female population varied slightly from 766-772. Initial female abundances were:

- Initial Abundance 1 (15% calves): calf = 112, yearling = 70, adult = 590
- Initial Abundance 2 (20% calves): calf = 150, yearling = 94, adult = 527
- Initial Abundance 3 (25% calves): calf = 187, yearling = 117, adult = 462

Model I Matrix:

$$\begin{pmatrix} 0 & M_y*R*S_{sc}*S_{wy} & M_a*R*S_{sc}*S_{wa} \\ S_{wc}*S_{sy}*S_{fy} & 0 & 0 \\ 0 & S_{wy}*S_{sa}*S_{fa} & S_{wa}*S_{sa}*S_{fa} \end{pmatrix}$$

Model II Matrix:

$$\begin{pmatrix} 0 & C_y*O*R*S_{sc}*S_{wy} & C_a*O*R*S_{sc}*S_{wa} \\ S_{wc}*S_{sy}*S_{fy} & 0 & 0 \\ 0 & S_{wy}*S_{sa}*S_{fa} & S_{wa}*S_{sa}*S_{fa} \end{pmatrix}$$

Figure 2-1. Leslie matrices constructed with two different fecundity calculations used in RAMAS Ecolab models to estimate population growth of cow moose in northern New Hampshire.

Results

Both Model I (λ=1.03) and II (λ=1.07) predicted finite rates of increase when using the actual survival rates measured in this study and fecundity data from marked (Model I) and harvested cows (Model II). Varying calf abundance had minimal effect on predicted populations in 2015. In Model I, the predicted cow population in 2015 ranged from 1050-1126 (25-15% calf abundance); Model II predicted a range of 1442-1489 cows, about 32% higher than Model I (Fig. 2-2 a).

Model I predicted a nearly stable growth rate (λ=1.01) and a 2015 population of about 860 cows when using the lower 95% confidence interval of winter calf survival. Model II predicted a growth rate of 1.03 and a 2015 population of about 1150 cows, about 34% higher than Model I (Fig. 2-2 b). When both lower calf and adult winter survival rates were used, both Model I and II predicted negative growth rates (λ=0.95 and 0.98) and population declines (5 and 2%). Predicted 2015 populations were <370 and <500, respectively (Fig. 2-3 a).

Model I predicted a negative growth rate (λ=0.97) and a 2015 population of about 610 cows when using the lower 95% confidence interval of yearling and adult survival in fall. Model II predicted a near stable growth rate of 1.01 and a 2015 population of about 870 cows, about 42% higher than Model I (Fig. 2-3 b). The elasticity and sensitivity analysis of all models indicated that population growth rate was most influenced by adult survival and least by yearling fecundity (Fig. 2-4).

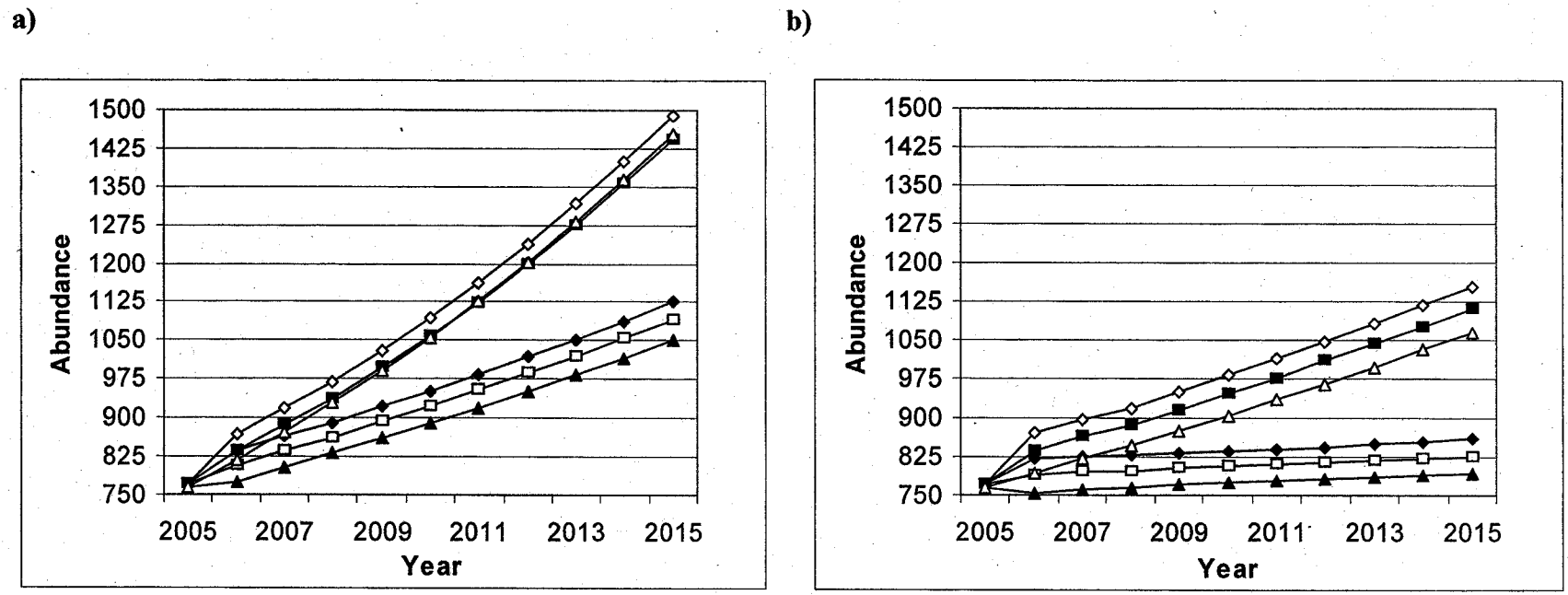


Figure 2-2. RAMAS Ecolab population trajectory models of cow moose in northern New Hampshire from Model I (radio-marked fecundity) and Model II (harvest fecundity) using (a) actual survival rates and (b) lower 95% confidence interval of winter survival rate of calves holding other survival rates constant.

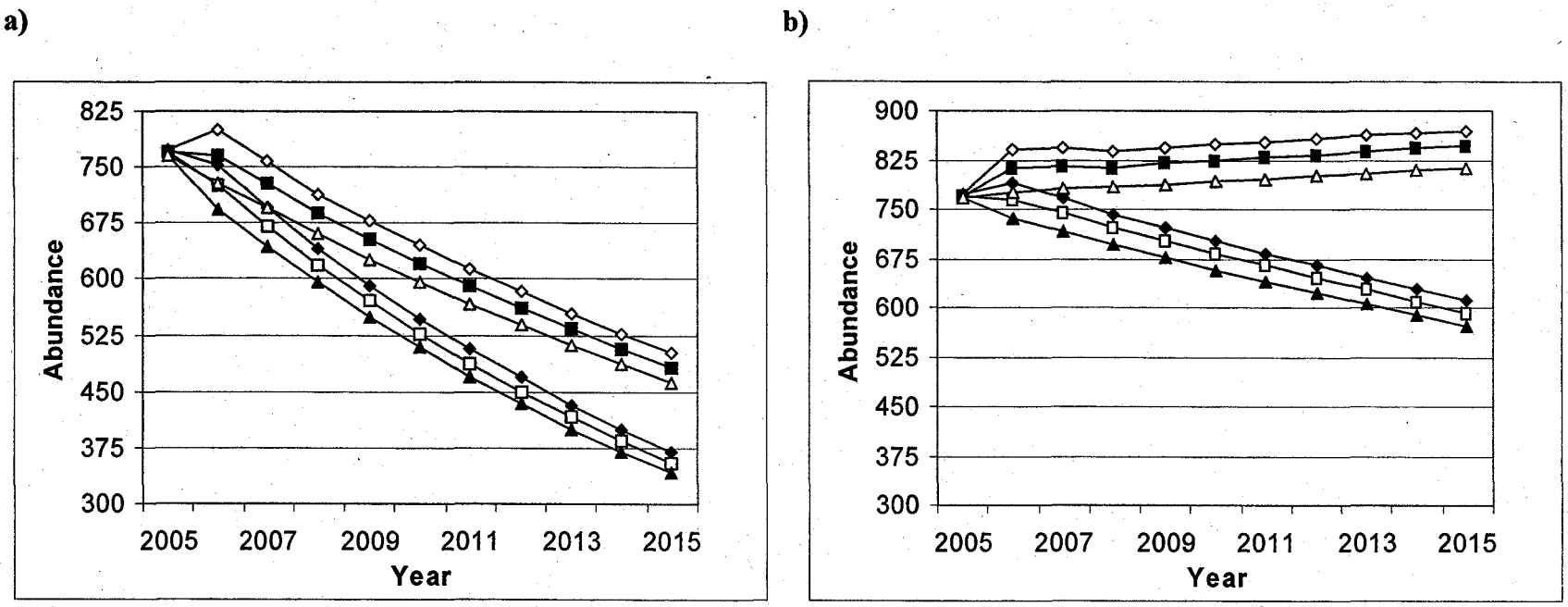
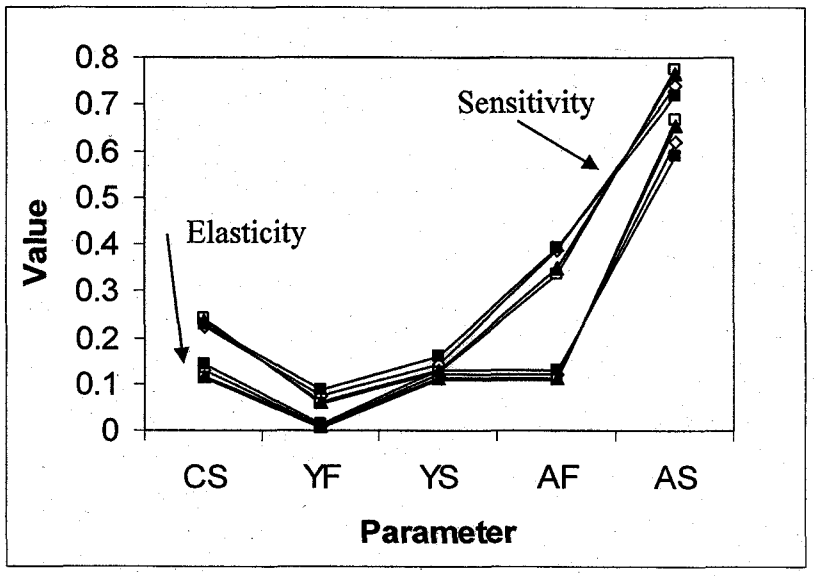


Figure 2-3. RAMAS Ecolab population trajectory models of cow moose in northern New Hampshire from Model I (radio-marked fecundity) and Model II (harvest fecundity) using (a) lower 95% confidence interval of winter survival rate of calves and yearling/adults and (b) lower 95% confidence interval of fall survival rate of yearling/adults holding other survival rates constant.

a)



b)

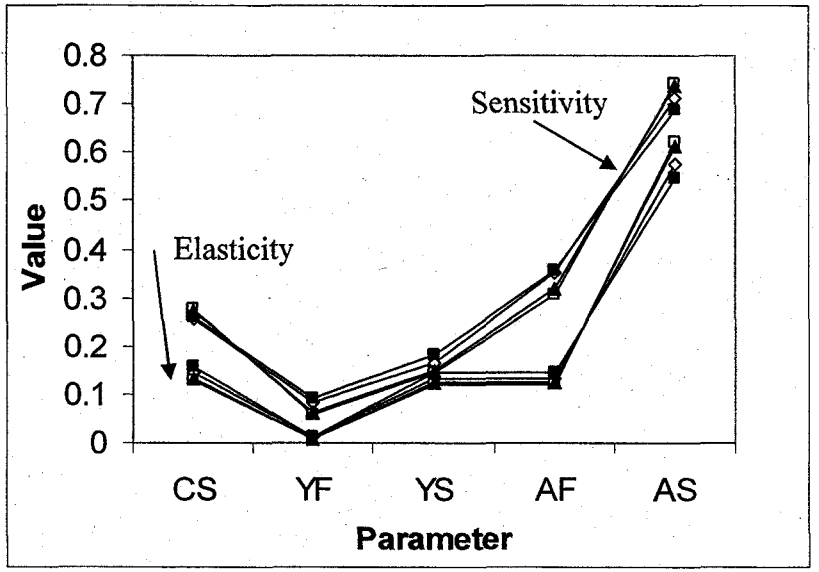


Figure 2-4. RAMAS Ecolab elasticity and sensitivity analysis of cow moose in northern New Hampshire from (a) Model I (radio-marked fecundity) and (b) Model II (harvest fecundity) where CS=calf survival, YF=yearling fecundity, YS=yearling survival, AF=adult fecundity, and AS=adult survival.

—◇— Actual survival
—□— Low calf winter survival
—▲— Low calf and yearling/adults winter survival
—■— Low fall yearling/adults survival

Discussion

Both models using survival rates from marked moose indicated that the moose population in northern New Hampshire should be growing at a moderate-low rate. Model II had the highest rate of increase (λ=1.07) but it was generally lower than in moose populations with similar characteristics. The average population growth rate of several North American moose populations with adequate food, limited predation, and minor harvest was 1.23 (range=1.15-1.30, Keith 1983). Populations with maximum fecundity, high adult (0.95) and calf survival (0.80), no emigration, and unstable age distributions could approach a growth rate of 1.42; populations in northern ranges that experience low calf survival cannot attain this rate (Van Ballenberghe 1983). In Sweden, growth rate ranged from 1.39-1.55 in an area with high moose density (2.3/km^2), few predators, and low non-hunting mortality; sex ratio rather than age class was considered most influential to growth because fecundity varied little among age classes (Cederlund and Sand 1991). Typically moose are abundant in single-predator systems (Messier and Crête 1985, Crête 1987, 1989, Bergerud and Snider 1988, Messier 1989); moose density was 1-2/km^2 where black bears were the only predator (Fryxell *et al.* 1988, Crête 1989).

The rate of population increase is most influenced by density-dependent factors such as age-specific survival, food competition, sexual maturation, litter size, and age-specific sex ratio (Van Ballenberghe and Ballard 1997). Dramatically reducing calf survival can cause substantial decline in population growth, conversely, high calf survival may offset low fecundity (Van Ballenberghe and Ballard 1997). In Newfoundland, a moose population with relatively low adult survival (0.75) and fecundity (0.4 calves/cow) remained stable due to high annual calf survival (0.67, Albright and Keith 1987). Severe

winters and, more importantly, tick epizootics resulting in substantial calf mortality could cause periodic, annual population decline. For example, reducing winter survival of calves from 0.67 to 0.53 produced a stable growth rate (λ=1.01) in Model I and minimal growth rate (1.03) in Model II. Conversely, high fecundity and favorable conditions for high calf survival increase recruitment and population growth. In a stable moose population in Alaska, annual declines occurred with increasing adult mortality and high summer mortality of calves resulting in low recruitment (0.11-0.22). Their models predicted a positive rate of increase (λ=1.21) when survival of calves, yearlings, and adults were increased, however, increasing fecundity to near theoretical maximum only increased λ from 0.99 to 1.04 (Testa 2004). Mathematically, survival of adult cows was the most influential factor in the models, however, survival rate was held constant in the models in determining rate of increase without annual variation. Therefore, winter survival of calves probably has more influence on annual population abundance than indicated by either model. Certainly calf survival and recruitment were the most variable parameter in the population.

Long-term studies of moose in North America suggest that populations erupt, crash, and then stabilize at various densities depending on current ecological conditions. Density-dependent effects normally regulate populations with lasting stability uncommon (Van Ballenberghe and Ballard 1997). Population dynamics models attempt to reliably estimate fluctuations in abundance and the factors ultimately responsible for change (Van Ballenberghe and Ballard 1997). However, actual abundance and predicted population growth rates often differ and likely reflect biased parameters in a model. New Hampshire has recently relied on observation rates of moose by deer hunters as a population index

which were related to moose density through infrared surveys but lacked accurate information on mortality and rate of change. Although observational data provides useful information of moose density, precision may be low without regular calibration with independent measurements of density (Ericsson and Wallin 1999, Sylvén 2000); a number of factors (e.g., weather, hunter access, habitat, and hunter bias) influence observation rates of moose (Crichton 1993). Additionally, survival rates were possibly overestimated due to sampling size or bias associated with the few marked yearling cows, and continuous monitoring of the same adult cows. Marked cows may have been less vulnerable to hunting, and older cows are probably more adept at avoiding vehicle collisions.

Although limited, dispersal may minimize population growth rate in northern New Hampshire. Density and social stress are important factors influencing dispersal and moose commonly emigrate from areas of high density to low density (Ballard *et al.* 1991). Short-range dispersal of moose is more common than long-range dispersal (Hundertmark 1997), with movements of cows up to 50-177 km (Mytton and Keith 1981, Ballard *et al.* 1991). Three cows dispersed from the study area with two long-term movements to the same area of southeastern Maine (~160 km) resulting in vehicle-collision mortalities. A dense population in Alberta had reduced growth rate (range=1.03-1.12) despite relatively high calf recruitment (0.44) and dispersal was suspected as the cause (Rolley and Keith 1980).

Modeling efforts with long-lived ungulates consistently indicate that adult survival has the greatest effect on population growth rate given stable fecundity, despite the importance of calf survival (Nelson and Peek 1982, Testa 2004). In most cases,

elasticity and sensitivity analysis of adult survival should be highest, although juvenile survival and reproduction are more variable (Gaillard *et al.* 1998). However, adult survival of large female ungulates normally has little annual variation, while annual survival of juveniles varies considerably indicating its substantial role in population dynamics. Moderate-high temporal variation in adult female survival is mostly associated with rare events such as epizootics which normally have short-lived effects on adult survival (Gaillard *et al.* 2000). Known-fate models (see Chapter II) for adults indicated variability between years and was most likely related to the only observed adult late winter mortality in 2002 due to tick-related and undetermined which caused annual survival to decrease by >10%. The sensitivity and elasticity analyses in this study predicted that adult cow survival was the most sensitive indicator to population change. Analysis may have been influenced because adults had no maximum age class in matrices and a constant adult survival and fecundity over 10 years (model time length) which are unrealistically high for adult cows beyond their prime. Population models essentially ignored annual variability in survival caused by such events as tick epizootics. Temporal variation in mortality and recruitment influences population dynamics of large herbivores and may be more important than elasticity or sensitivity in determining relative changes in demographic parameters (Gaillard *et al.* 2000). While abnormal adult tick-related mortality should have an impact on annual population growth, the frequency of tick epizootics may be the most important factor in relation to other sources of mortality in New Hampshire.

Low-moderate levels of tick-mortality in calves should normally be expected, however elevated mortality may be observed during epizootic years. Therefore, it was

theorized that the temporal variation associated with tick mortality in calves could have the greatest influence on population growth. Although in 2002 of this study calf survival was lowest (0.49) compared to 2003-2004 (0.68-0.71), the known-fate models (see Chapter II) indicated little support for annual variability which could have been due to small sample size because of excessive collar loss. Therefore, it cannot be stated that temporal variation in calf survival alone has the greatest influence on population growth. However, calf survival in New Hampshire probably has the potential to vary more year to year compared to adult survival because winter ticks have the greatest and most frequent influence on calves. This could be further verified by continued research.

Calves accounted for 88% of tick-related mortality in this study and survival analysis indicated that winter calf survival for all years was dependent on late winter when tick-related deaths occurred most (88%). Juveniles account for much between-year variation in population growth rate and their influence may increase with environmental severity (Clutton-Brock *et al.* 1985, Van Sickle 1990, Hatter and Janz 1994, Gaillard *et al.* 2000). Adult survival, with typically low temporal variation and high elasticity, may not have the greatest influence relative to vital rates of juveniles with high temporal variation and low elasticity (Gaillard *et al.* 2000). The low elasticity of vital rates of juveniles may be overwhelmed by the high temporal variation of those rates, therefore, this effect on population dynamics should not be underestimated (Gaillard *et al.* 2000). The perceived stability of the local population probably reflects the high variation in mortality caused by periodic tick epizootics which results in abnormal mortality of yearling/adults and elevated calf mortality. However, the influence of winter tick on calf survival, recruitment, and yearling productivity may have the greatest impact on annual

population abundance.

Management Implications

Moose have high economic value in New Hampshire because they are an important source of revenue related directly to hunting and ecotourism. This study presented the first assessment of the dynamics and potential limiting factors of the moose population in northern New Hampshire. The data revealed that habitat quality, winter severity, and predation are not limiting factors of the population, however, parasite-related mortality and increased age of first reproduction are probably strong determinants of population growth and stability. The temporal variation of winterkill/parasite-related mortality is certainly a significant factor in population dynamics in the study area, and likely throughout New Hampshire. The mechanisms influencing this source of mortality are not adequately understood, and likely impossible to manage, but their impact could be predictable.

The population modeling indicated that there should be a positive finite rate of increase within the study area based on data collected from radio-marked moose, however, a stable or declining growth rate is predicted in years of high calf mortality alone, or combined with mortality of yearling/adults. Therefore, temporal trends in demographic patterns, most importantly winter mortality, should be closely monitored. Additional long-term radio-marked studies would provide accurate data but may not be feasible. Aerial surveys used to estimate recruitment from cow:calf ratios prior to moose shifting to coniferous habitat in mid-winter would not document typical winterkill/parasite mortality. However, aerial surveys could be used to quantify hair loss and damage late winter to predict tick abundance and potential tick-related mortality but

may not be feasible (Samuel and Welch 1991, Garner and Wilton 1993). Spring ground surveys in known moose wintering areas similar to winter deeryard surveys could possibly provide mortality estimates from carcasses with tick-related evidence (e.g., hair loss, remaining ticks, %FMF). Surveys could possibly be implemented by, and targeted towards NHFG staff, shed-antler hunters, trappers, loggers, and outdoor recreationists that are afield during snowmelt prior to green-up in April. Spring and fall weather conditions could also prove valuable as indices to forecast tick epizootics. Little to no snow cover, and warmer than normal temperatures in both April and October-December might correlate with increased tick density and high moose mortality. More data are needed to identify the role of weather patterns in tick epizootics.

Additional research on the effect of the winter tick on moose population dynamics is warranted given questions generated from this study; 1) What effect does an infestation have on yearling productivity and adult twinning? 2) Are birth weight and body condition of calves affected by tick infestations of cows? 3) Can tick epizootics be accurately forecasted from moose density, snow cover, and fall and spring weather conditions?

Calves are most susceptible to winter tick-related mortality, however, elevated mortality may be associated with adults in poor condition and predisposed to mortality from heavy tick infestations. Determining the frequency of epizootics is the most important for moose managers. Further, yearlings may not achieve sufficient body weight required for ovulation due to infestation of winter tick. Monitoring of yearling and adult field-dressed weights and ovulation rates should continue to identify annual trends and predict population status.

CHAPTER III

METABOLIC IMPACTS OF WINTER TICK INFESTATIONS ON CALF MOOSE

Introduction

Moose (*Alces alces*), elk (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*) are the three main hosts of the winter tick (*Dermacentor albipictus*) which is found throughout much of North America. Moose are the most severely affected host from infestations of winter ticks that can cause anemia, hair loss and damage, reduced fat stores, reduced feeding, excessive grooming, restlessness, and reduced growth in calves (Welch *et al.* 1991, Samuel 2004). Weather and environmental conditions largely influence seasonal and annual populations of winter tick (Drew and Samuel 1986, Samuel and Welch 1991, Wilton and Garner 1993, Samuel 2004). Substantial moose mortality in conjunction with heavy tick infestations has been reported throughout North America including Alberta (Samuel and Barker 1979), Minnesota (Lenarz 1992), Algonquin Provincial Park in Ontario (Garner and Wilton 1993), and most recently, widespread in Canada in 1998-1999 (Samuel 2004), and throughout western Canada, Maine, Vermont, New Hampshire, and Isle Royale in 2001-2002 (Samuel and Crichton 2003). Despite the relationship between winter tick infestations and specific moose die-offs, the role of winter ticks in regulation of moose populations has not been established (Van Ballenberghe and Ballard 1997, Samuel 2004).

Calves are the most susceptible cohort during die-offs associated with winter ticks; anemia is suspected as the primary factor of mortality (Samuel 2004). Moose calves must maintain an adequate blood energy level for growth and maintenance during winter. The large volume of blood loss associated with heavy tick infestation negatively influences a calf's nutritional status in March-April when forage has low nutritional quality and digestible protein (Samuel 2004). Calves are in poorest condition at winter's end and animals on a lower nutritional plane generally carry more ticks (Gladney *et al.* 1973).

In captive moose calves, high numbers of ticks caused reduced weight gain and chronic weight loss (Glines and Samuel 1989, Addison *et al.* 1994), extensive hair loss and decline in visceral fat (McLaughlin and Addison 1986), and hypoalbuminemia and anemia (Glines and Samuel 1989). A moderate tick load (*Rhipicephalus appendiculatus*) on livestock calves reduced annual weight gain by 10-44 kg due to blood loss and tick-induced anorexia; larvae and nymphs had negligible effect compared to engorging, adult female ticks (Norval *et al.* 1988).

The effect on host fitness associated with blood removal by ectoparasites has been studied in birds (Gold and Dahlsten 1983, Roby *et al.* 1992, Simon *et al.* 2003), reptiles (Wikelski 1999), small mammals (Khokhlova *et al.* 2002), and livestock (Seifert *et al.* 1968, Springell *et al.* 1971, Corrier *et al.* 1979, Norval *et al.* 1988). These studies indicated that blood consumption by parasites has varying effects on blood protein, weight gain, behavior, productivity, and metabolic rate of hosts. Behavioral responses associated with tick-induced hair loss and grooming have negative energetic consequences in moose (McLaughlin and Addison 1986, Addison and McLaughlin 1988,

Welch *et al.* 1990, Samuel 1991, Mooring and Samuel 1999, Samuel 2004), although few studies have investigated the relationships among tick infestation, blood loss and metabolic balance in wild ungulates.

After hatching in late summer, "seed ticks" ascend vegetation to form clumps of larvae in September-October where they wait or "quest" for a host (Samuel 2004); however, larvae can survive well past November depending on weather conditions (Samuel and Welch 1991). By November, larvae molt to nymphs subsequent to their first blood feeding and remain dormant on the host until late January when they molt to adults after the second blood meal in late January-March. Adults peak in number and size in March and April, continue to feed, mate on the host, and eventually drop off by early May, whereupon engorged female ticks lay their eggs in leaf litter; moose are tick-free throughout summer (Samuel 2004).

Tick disengagement occurs during a 9-10 week period between late February and mid-May, peaking in late March and early April (Drew and Samuel 1989). The duration of feeding for several species of adult female ixodid (hard body) ticks ranges from 6-13 days and blood removal can equal 3.0-7.5 times their engorged body weight (Sonenshine 1991). Depending on the species and host, engorgement is completed within several days with a large volume of blood loss during the last 24-36 hours of feeding (Sonenshine 1991). Blood concentration in the cattle tick (*Boophilus microplus*) was greatest during the last hours of final feeding when engorged females consumed a concentrated blood meal twice their own weight (Seifert *et al.* 1968).

The relationship between tick infestation and mortality of moose calves is evident, however, the physiological impact on their energy and protein balance has not been

estimated quantitatively. Such estimates are useful to better understand and predict mortality associated with winter tick infestations. The objectives of this study were to estimate total blood volume removal by adult female winter ticks on moose calves at variable levels of infestation, and to estimate energy and protein deficits associated with this blood loss.

Methods

Metabolic impacts of blood loss were estimated with models that incorporated variable calf weights, levels of tick infestation, weight of engorged ticks, and timing of feeding. Calf weight in March-April was set at 150 and 175 kg (Addison *et al.* 1994, Samuel 2004). Tick infestation level was set as 10,000 (low), 30,000 (moderate), 50,000 (high), and 70,000 (severe) ticks (W.M. Samuel pers. comm.). The number of adult females at each infestation level was estimated as 25.6% of the total tick load as measured on calves in March-April (Samuel 2004). Larvae, nymphs, and adult males were not considered in the analysis because they consume relatively little blood compared to adult females (Sonenshine 1991, Samuel 2004).

Engorged weights of adult female ticks have been estimated at 0.61 (Glines 1983) and 0.85 g (Addison *et al.* 1998a); a conservative estimate of 0.50 g was used to account for ticks not fully engorged due to early removal by grooming (Samuel 2004). Total amount of blood loss per adult female tick is greater than the final engorged weight because undigested blood can be ≥2X that of the final engorged weight (Sonenshine 1991, Samuel 2004); therefore, blood loss was estimated as 2 and 3X engorged weight. Drew and Samuel (1989) measured that tick drop-off in moose calves experimentally infested with 30,000 larvae primarily occurred from March-April, peaking between 20

March-6 April. In this study, the drop-off period and total blood loss was estimated over an 8- period between 1 March-25 April; 15% in weeks 0-2, 25% in weeks 2-4, 50% in weeks 4-6, and 10% during the final 2 weeks.

Vertebrate blood contains approximately 15% hemoglobin and 7% plasma proteins (Sonenshine 1991). Hemoglobin and total plasma protein in blood of moose calves during late winter average 0.17 and 0.06 g/mL, respectively (Franzmann and LeResche 1978). I assumed a conservative value of 0.20 g protein/mL of blood, 4.3 kcal/g protein (Schmidt-Nielson 1997), and a metabolic efficiency of 75% in replacing blood (Blaxter 1989); energetic cost of replacing blood was subsequently estimated as 1.15 kcal/mL. Daily protein requirements were assumed as 168 and 189 g protein/day for 150 and 175 kg calves, respectively (Schwartz *et al.* 1987b, Robbins 1993). Total blood volume was estimated as 8% of body weight (Samuel 2004); calves weighing 150 and 175 kg had blood volumes of 12000 and 14000 mL, respectively. The daily metabolizable energy requirements for maintenance of a calf was assumed as 134 $kcal/kg^{0.75}/d$ (Cool and Hudson 1996), which equaled 5743 and 6447 kcal/d for a 150 and 175 kg calf, respectively.

Results

Total blood loss at the low infestation level (10,000 ticks) was estimated as 2560 and 3840 mL for 2 and 3X engorged weight, respectively; total blood loss at the severe infestation level (70,000) was 17920 and 26880 mL, values exceeding total blood volume (Fig. 3-1). Percent total blood volume lost in 150 and 175 kg calves in low-severe infestations ranged from 21-224% and 18-192%, respectively; percent daily blood loss ranged from 0.4-4.0% and 0.3-3.4%, respectively. Percent total blood volume lost in 150

and 175 kg calves from low-severe infestations during weeks 4-6 ranged from 11-112% and 9-96%, respectively; percent daily blood loss ranged from 0.8-8.0% and 0.7-6.9%, respectively (Table 3-1).

The energy cost to replace blood loss ranged from 2944-20608 kcal at 2X engorged weight at low-severe infestation levels, and 4416-30912 kcal at 3X engorged weight (Fig. 3-2). The percent deficit of the daily energy budget for a 150 kg calf ranged from 0.9-9.6% for low-severe infestations at 0-8 weeks and 1.8-19.2% at weeks 4-6; the estimates for a 175 calf were estimated at 0.8-8.6% and 1.6-17.1% (Table 3-2).

Total protein lost during low-severe infestations ranged from 512-3584 and 768-5376 g at 2 and 3X blood-fed weight, respectively (Fig. 3-3). Daily protein loss at a moderate infestation level (30,000) and 2-3X blood-fed weight was 11.0-16.5 g during weeks 6-8 and 54.9-82.3 g during weeks 4-6. Daily protein loss associated with 70,000 ticks peaked during weeks 4-6 and exceeded the daily protein requirement of 150 and 175 kg calves (Fig. 3-4). During weeks 2-6, daily protein loss was 50-100% of the daily protein requirement (Fig. 3-4). As a percent of the daily protein requirement, protein loss of a 150 kg calf peaked at 33-49% at a moderate infestation level, and 76-114% at a severe infestation level in weeks 4-6; a 175 kg calf peaked at 29-44% at a moderate infestation level, and 68-102% at a severe infestation level in weeks 4-6 (Fig. 3-4).

Discussion

It was theorized that blood removal by winter ticks could have substantial physiological consequences for moose calves in late winter-early spring. This exercise, performed with conservative estimates, indicated that blood loss associated with high-severe tick infestations has substantial impact on energy and protein balance in moose

Table 3-1. Total and (daily) percent blood volume of calf moose removed by engorging adult female ticks. Infestation level, stage, engorged weight (2 and 3X), and calf weight were varied; total blood volume was estimated as 8% of body weight (Samuel 2004).

Infestation Level	150 kg		175 kg	
	100% Week 0-8	50% Week 4-6	100% Week 0-8	50% Week 4-6
10,000				
2X	21 (0.4)	11 (0.8)	18 (0.3)	9 (0.7)
3X	32 (0.6)	16 (1.1)	27 (0.5)	14 (1.0)
30,000				
2X	64 (1.1)	32 (2.3)	55 (1.0)	27 (2.0)
3X	96 (1.7)	48 (3.4)	82 (1.5)	41 (2.9)
50,000				
2X	107 (1.9)	53 (3.8)	91 (1.6)	46 (3.3)
3X	160 (2.9)	80 (5.7)	137 (2.4)	69 (4.9)
70,000				
2X	149 (2.7)	75 (5.3)	128 (2.3)	64 (4.6)
3X	224 (4.0)	112 (8.0)	192 (3.4)	96 (6.9)

Table 3-2. The cost of replacing blood removed by engorging adult female ticks as a percent of the daily metabolizable energy requirement of moose calves. Infestation level, stage, engorged weight (2 and 3X), and calf weight were varied; total blood volume was estimated as 8% of body weight (Samuel 2004).

	150 kg		175 kg	
Infestation Level	100% Week 0-8	50% Week 4-6	100% Week 0-8	50% Week 4-6
10,000				
2X	0.9	1.8	0.8	1.6
3X	1.4	2.7	1.2	2.4
30,000				
2X	2.7	5.5	2.4	4.9
3X	4.1	8.2	3.7	7.3
50,000				
2X	4.6	9.2	4.1	8.2
3X	6.9	13.7	6.1	12.2
70,000				
2X	6.4	12.8	5.7	11.4
3X	9.6	19.2	8.6	17.1

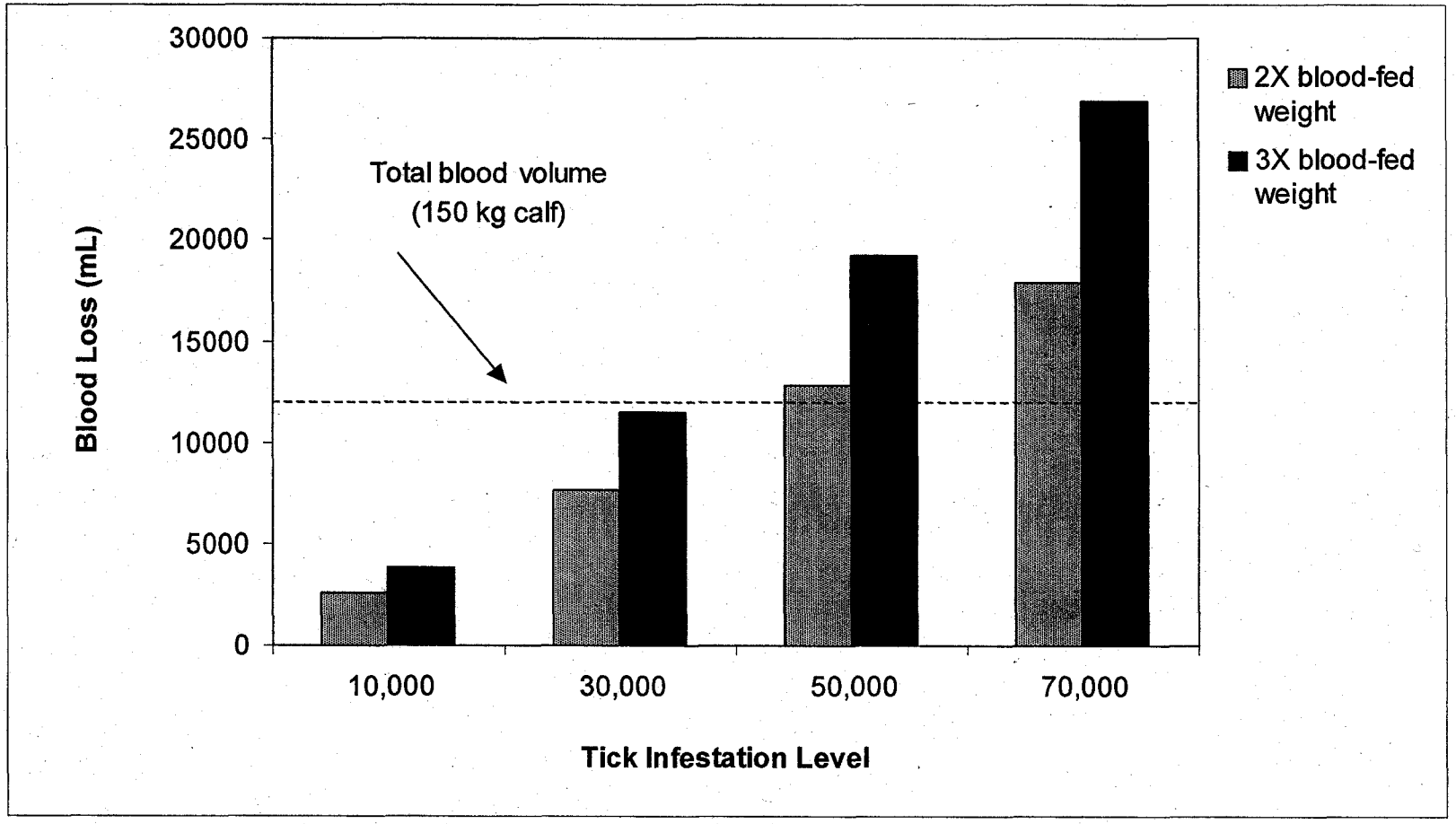


Figure 3-1. Total blood removal by adult female winter ticks at low-severe infestation levels on moose calves over the 8-week engorgement period.

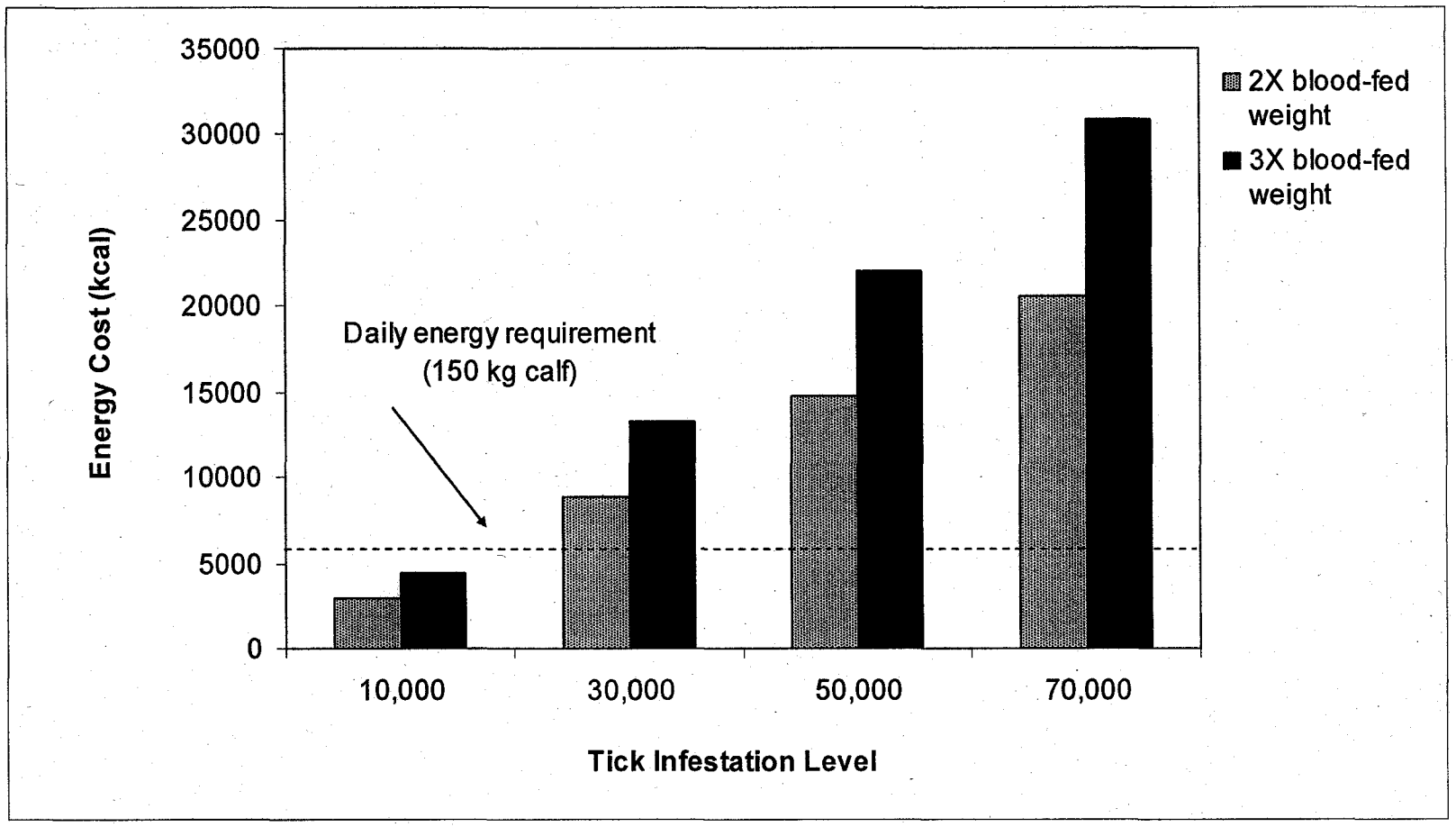


Figure 3-2. Total energy cost for moose calves to replace blood loss at low-severe infestation levels of adult female winter ticks over the 8-week engorgement period.

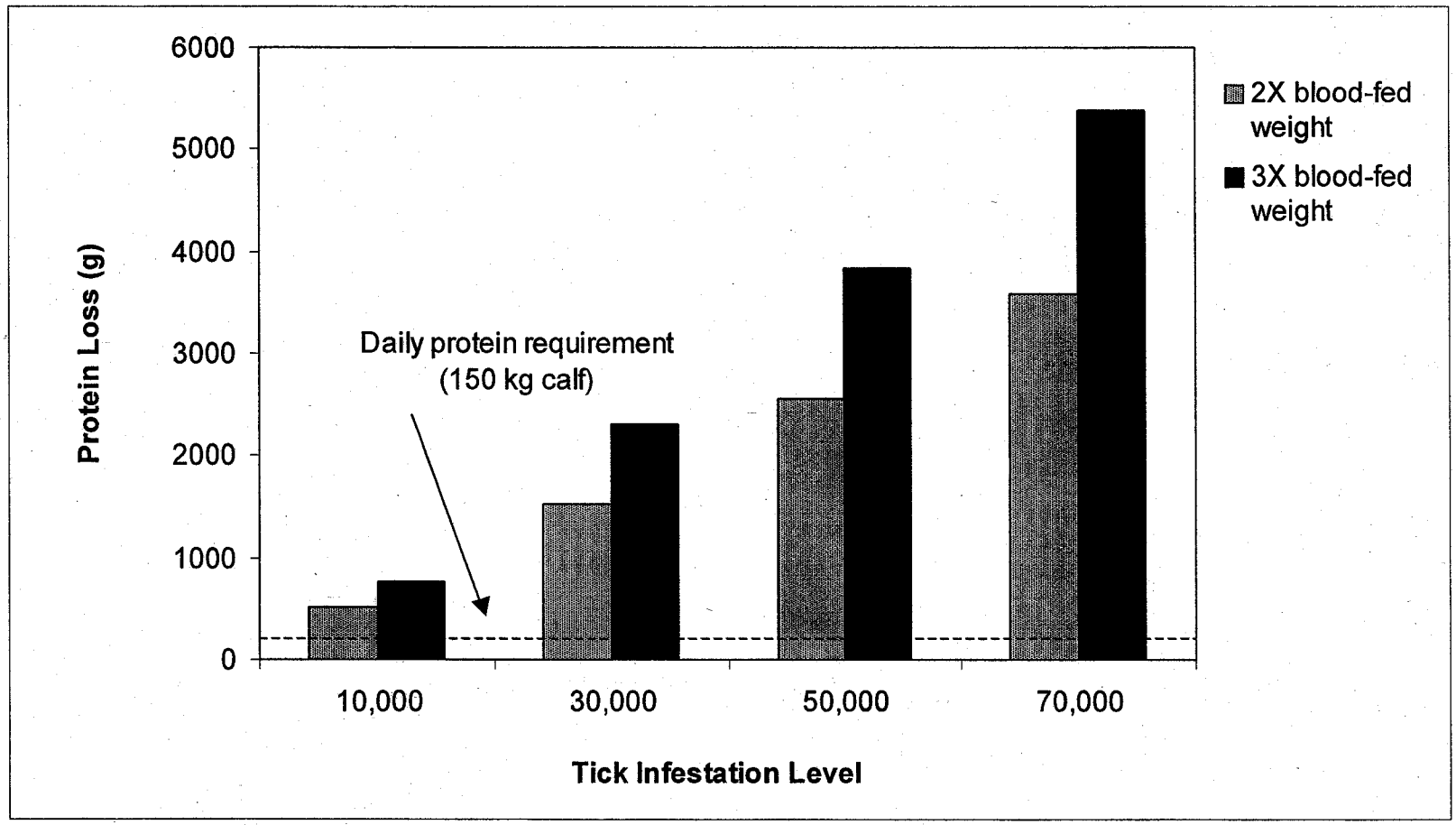


Figure 3-3. Total protein cost for moose calves to replace blood loss to adult female winter ticks at low-severe infestation levels over the 8-week engorgement period.

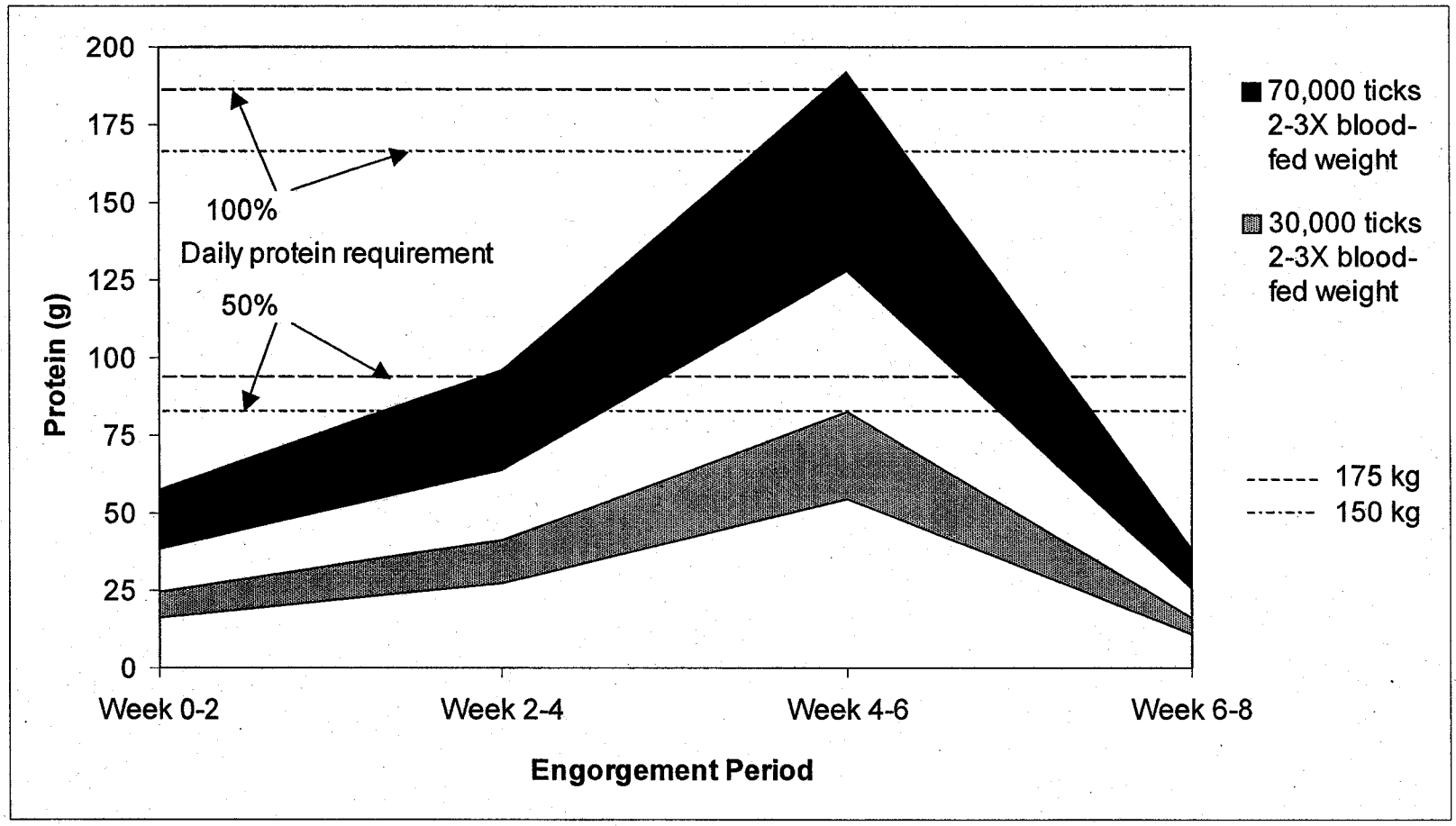


Figure 3-4. Daily protein loss in moose calves associated with blood loss at moderate and severe infestation levels of adult female winter ticks over the 8-week engorgement period.

calves. The physiological impact of blood removal by adult female ticks extends for approximately 8 weeks, and calves likely experience chronic, and eventually acute anemia during peak engorgement by weeks 4-6 during early-mid April. Anemia associated with blood removal by ticks is well recognized in cattle (Francis 1960, O'Kelly and Seifert 1969, Corrier *et al.* 1979) and more recently in moose (Glines and Samuel 1989, Samuel 2004). Hemorrhagic anemia caused by parasites occurs when the balance between blood loss and production is not maintained (Samuel 2004). Calves unable to compensate for blood loss would be nutritionally deficient and more susceptible to late winter mortality.

During winter moose attempt to minimize physiological decline as opposed to growth, and as a consequence of their age and smaller body size, calves have higher metabolic demands than adults on a relative scale (Schwartz *et al.* 1991). Stored body fat and protein allow moose to survive normal energetic deficits in late winter (Schwartz and Renecker 1997), however, calves are more susceptible to late winter mortality because they have proportionally less fat reserves due to their smaller size and higher physiological priority for growth (Van Ballenberghe and Ballard 1997). During late winter moose consume forage of minimal nutritional value and the relative energetic cost associated with compensating for blood loss is presumably higher for animals in poor condition, especially calves (Lankester and Samuel 1997, Samuel 2004).

Livestock calves infested with ticks (*Rhipicephalus appendiculatus* and *Boophilus microplus*) suffered 38-44 kg in weight loss (Corrier *et al.* 1979, Norval *et al.* 1988). Moose calves severely infested or in weakened condition are probably unable to sustain the energetic demand needed for blood regeneration and consumption of adequate food

resources. Volume of daily blood loss was an important factor in the mortality of smaller, tick-infested livestock calves compared to larger surviving calves (Corrier *et al.* 1979). Because weights of engorged female ticks were higher on moose that groomed less and were sickly (Drew and Samuel 1989), calves in poor condition may experience more pronounced energy and protein deficits.

For example, the daily percent loss of total blood volume during weeks 4-6 ranged from 2.0-3.4% and 4.6-8.0%, respectively, during moderate and severe tick infestations of 30,000-70,000 ticks (Table 3-1). Calves infested with ≥50,000 ticks would lose 1-2X their blood volume over the 8-week engorgement period. Guidelines for blood collection of healthy animals on an adequate nutritional plane suggest that 10% of blood volume can be taken every 3-4 weeks or 1% daily for repeated bleeds at shorter intervals (Morton *et al.* 1993). Further, total blood loss as a percent of total blood volume during weeks 4-6 ranged from 27-48% and 64-112%, respectively (Table 3-1). Most animals experience hemorrhagic shock if 30-40% of blood volume is removed over a short period of time, and >40% removal may cause death (McGuill and Rowan 1989).

The percent of the daily metabolizable energy requirement required to replace the average daily blood loss during the engorgement period ranged from 2.4-4.1% and 5.7-9.6% in moderate and severe infestations (Table 3-2). However, the daily estimates during weeks 4-6 were much higher, 4.9-8.2% and 11.4-19.2%, respectively. These additional energy costs would increase the daily energy deficit normal at end of winter, accelerate nutritional decline and weight loss, and likely cause increased physiological stress related to concurrent anemia.

Calves normally experience a negative energy balance in winter when the

metabolizable energy requirement exceeds forage intake energy; calves sustain a daily energy deficit of 43% in winter assuming availability of good quality dry matter forage (2.2 kcal/g of metabolizable energy) and a daily consumption rate of 1% body weight (Schwartz and Renecker 1997). Calves infested with 70,000 ticks would lose an equivalent of 3-5 days of metabolizable energy requirement over the 8-week engorgement period. Increased grooming and less time spent feeding during March-April accentuate the negative energy balance at the end of winter (McLaughlin and Addison 1986, Addison and McLaughlin 1988, Samuel 1991, Mooring and Samuel 1999, Samuel 2004). Although the role of protein metabolism may have the strongest influence on calf survival, the constant energy cost associated with blood replacement adds to the negative impact of ticks.

Low tick loads had minimal effect on hematological parameters of captive moose maintained on a diet of 16% protein (Addison *et al.* 1998b); however, winter browse typically has 5-7% protein and is poorly digested (Schwartz and Renecker 1997). Conversely, poor nutrition reduced hematological values for cattle lightly infested with *Boophilus microplus* when compared to animals on an adequate diet (O'Kelly *et al.* 1971), and tick-infested cattle versus tick-free cattle, had reduced levels of hemotacrit, hemoglobin, serum albumin, and total protein (O'Kelly and Seifert 1969). Alexander and Kiesel (1965) reported that blood loss coupled with low protein diet (8%) adversely affected weight gain, hemoglobin, and hematocrit in lambs; minimal effects occurred in lambs maintained on a 16% protein diet.

The protein deficit associated with blood loss and regeneration is probably the most critical physiological problem for calves. In this exercise, daily protein loss of 50-

>100% of the daily protein requirement of moose calves occurred for 4 continuous weeks (weeks 2-6, Fig. 3-4). Losses were most pronounced during weeks 4-6; 29-49% in a moderate infestation and 68-114% in a severe infestation (Fig. 3-4). Calves infested with 70,000 ticks would lose an equivalent of 3-4 weeks of the daily protein requirement. Compensation would be problematic because the engorgement period occurs prior to spring green-up and they are invariably in an energetic deficit and losing weight (Schwartz *et al.* 1988); calves experiencing severe levels of blood loss should be considered at high-risk for mortality from anemia and associated effects.

A majority of patho-physiological studies of ruminants infested with gastrointestinal nematodes have emphasized that protein metabolism is much more disturbed than energy (Bown *et al.* 1991). The negative impact and host-susceptibility of nematode parasitism in ruminants can be greater for malnourished animals and effects can be reduced by a high protein diet (Van Houtert and Sykes 1996, Coop and Kyriazakis 2001). Because moose calves will invariably be in poor nutritional condition and forage quality will be limited during the adult tick engorgement period, their ability to survive tick infestations is probably most influenced by their nutritional status and the level of infestation.

The estimated proportion of adult female ticks on adult moose during late winter is lower on cows (18.0%), and slightly higher on bulls (27.6%), relative to calves (25.6%) (Samuel 2004). With similar calculations as used with calf estimates, the percent daily energy budget deficit for a cow (360 kg) during weeks 4-6 with a moderate infestation level was 1.9-2.9%, and a bull (400 kg) 2.7-4.1%, whereas a severe infestation level produced a daily deficit of 4.5-6.7% for a cow and 6.3-9.5% for a bull. During weeks 4-

6, the percent deficit of the daily protein requirement for a cow was 11.9-17.9% at a medium infestation level and 27.8-41.7% at a severe infestation level. Daily protein deficit for a bull ranged from 16.8-25.3% and 39.3-59.0%. Daily losses in adults as a proportion of the energy budget and protein requirement were 50-70% less than those estimated for calves. Undoubtedly calves are most susceptible to winter tick-related mortality, however, adults in poor condition may be predisposed to mortality from heavy tick infestations, although adults probably survive in most circumstances. These "baseline" estimates for adults could have greater fitness consequences by compounding the costs of pregnant (last trimester) cows and bulls suffering from the rut.

Mortality associated with winter ticks in this study (see Chapter II) was highest in April (75%) corresponding to weeks 4-6 of tick engorgement when blood loss was greatest and most concentrated. The average tick abundance on moose in western Canada was estimated as 33,000 with 19% having >50,000 and 6% >80,000 (Samuel 2004). Although tick density was not measured on calf mortalities in this study, hair loss and damage was most severe on carcasses in 2002 when calf survival was lowest (0.49) and the highest percentage of winterkill/parasite mortality occurred; regional spikes in spring mortality (Samuel and Crichton 2003) and severe coat damage to non-study moose were concurrent. It was assumed that tick abundance peaked and was high-severe in 2002 and was low-moderate in 2003-2004 when calf survival was 0.70 (see Chapter II). In addition to high-severe levels of infestation and tick-related hair loss/damage, a majority of the radio-marked calf mortalities were emaciated, had poor body fat, 16.5% mean femur marrow fat, had secondary infestations of lungworm (*Dictyocaulus viviparous*), and had noticeable paleness of eye mucous membranes which is a

characteristic of anemia in domestic ruminants (Kaplan *et al.* 2004).

In conclusion, this exercise indicated that blood loss to winter ticks alters protein and energy metabolism of moose calves substantially, and likely influences their fitness and survival. Heavily infested calves are more susceptible to late winter mortality, however, the effect of a moderate infestation may be amplified by secondary infestations of lungworm, severe winters, and/or poor body condition. The effect of chronic blood loss is exacerbated by a low protein diet, and as a result, calves are unable to adequately replace protein loss and become anemic. Models potentially mask the effects associated with more synchronous and concentrated blood loss. Therefore, it is evident from these conservative estimates and the pattern of calf mortality in this study that winter tick infestations have considerable influence on calf survival and population dynamics of the study moose population.

Management Implications

April is a critical month for moose calves and winterkill/parasite-related mortality is an important factor in the winter survival of calves in the study area, and likely throughout northern New Hampshire. The current exercise presented an experimental assessment of the metabolic consequences of blood loss incurred by tick-infested moose calves. Protein deficiency caused by anemia from heavy tick infestations is hypothesized to be the primary factor causing late winter calf mortality.

Factors influencing this source of mortality are not adequately understood but may be predictable. Although difficult to manage in New Hampshire, habitat quality in the study area appears good and adequate for winter survival. However, temporal trends of winter mortality and seasonal weather conditions should be closely monitored. Aerial

surveys are often used to quantify hair loss and damage on moose in late winter to predict tick abundance and potential tick-related mortality (Samuel and Welch 1991, Garner and Wilton 1993), but may not be feasible or practical in New Hampshire. Spring ground surveys could possibly provide estimates of winterkill/parasite mortality of calves and document carcasses with tick-related evidence (e.g., hair loss, remaining ticks, femur marrow fat %). Surveys could be targeted towards NHFG staff, shed-antler hunters, trappers, loggers, and outdoor recreationists that are afield during snowmelt prior to green-up in late April (Garner and Wilton 1993).

Spring and fall weather conditions might prove valuable as indices to forecast tick epizootics. Little to no snow cover, and warmer than normal temperatures in both April and October-December, might correlate with increased tick density and high moose mortality. Initiating a spring mortality survey and monitoring fall and spring weather and snow patterns may provide simple and economical methods for documenting and predicting mortality associated with tick infestations. During years when weather patterns indicate optimal conditions for high tick abundance, increased late winter mortality of calves could be expected. However, the interrelationships of weather, tick abundance and survival, habitat conditions and dynamics, fitness, and other physical and physiological factors affecting moose populations suggest that a simple predictive relationship is unlikely.

SUMMARY

This study was designed to investigate the characteristics and dynamics of a moose population in northern New Hampshire. This population was perceived as stable despite favorable habitat and conservative harvest. The study area was approximately 1000 km² located centrally in the town of Berlin within NHFG WMUs B, C1, and C2. The study took place in 2002-2005 with captures occurring Decembers 2001-2003. Of 96 moose captured, 81 were net-gunned and 15 darted; 92 moose (33 adults, 59 calves) were radio-marked successfully with VHF (n=83) or breakaway GPS (n=9) radio-collars.

Radio-marked cows were stalked and observed 2-3 times weekly from 1 May-1 July, and weekly thereafter until 15 August, 2002-2005 to measure parturition, fecundity, and calf survival. Parturition (n=77) ranged from 8 May-13 July with a median date of 19 May; it was highly synchronous with 78% of births occurring from 13-27 May. The annual consistency of parturition dates and relatively high calf survival (0.71) in the first two months of age probably reflect the relationship between abundant forage resources and high energetic requirements associated with lactation and rapid growth of calves. The annual calving rates of yearlings and adults (≥2 yr) averaged 30 and 85%, and 21 of 28 adult cows observed more than one calving season had a calf in consecutive years; the yearling rate was considered low whereas the adult rate was similar to the mean rate in North America. The twinning rate of 11% was considered low; two adult cows had twins in multiple years (2 and 3 years) suggesting that twinning may be a phenotypic trait.

In addition to reproductive data of radio-marked cows, data from harvested adult

cows (1988-1998) were used to evaluate productivity. From 1988-1998 to 1999-2004, the average field-dressed weight of adult cows increased, the mean age (~5 yr) remained within the optimal range of productivity, ovulation rate remained >90%, and the number of CL/cow declined slightly both in the study area (1.44-1.24) and statewide (1.36-1.22). In the same time period ovulation rates (41-42%) of yearlings in the study area and statewide declined about 25% and their average field-dressed weight declined 4% to 210 kg in the study area and 204 kg statewide. Productivity is often related to habitat quality, however the temporal trends of reproductive characteristics and body weights of yearling and adult cows suggests that habitat quality is probably not limiting to the population.

Radio-marked moose were monitored every 1-3 days with a combination of aerial and ground telemetry, and direct observation to measure mortality. Necropsies were performed to establish probable cause of death. There were 39 mortalities (19 calves, 6 yearlings, and 14 adults) with 41% occurring in April and 21% in October. Winterkill/parasite (41%), vehicle collision (26%) with most (60%) at roadside salt licks, and hunting (18%) were the three major causes of mortality.

Survival analysis of both marked moose and unmarked calves was conducted using program MARK v.4.2. The major causes of mortality of radio-marked cows were human-related and survival (0.87) was similar to populations with limited to no predation. Excluding early winter when no mortality occurred, weekly survival was similar among seasons although fall was slightly lower (0.94) because of harvest mortality. Annual variation in survival (2002-2004) was due to late winter mortality from winterkill/parasite and unknown cases in April 2002 that reduced annual survival by >10%. Although survival of female adult ungulates is normally high relative to juveniles,

periodic tick epizootics represent the only measurable natural mortality of adult cow moose in northern New Hampshire.

Calf survival increased with calf age and was not dependent on date of birth or higher for calves born during peak parturition. Survival of unmarked calves 0-2 months of age was relatively high (0.71) compared to predator-regulated populations, but somewhat lower than in populations with few to no predators. Cause of death was unknown, but similar timing (76% in first 28 days of life) of mortality each year suggested that the cause was consistent and probably black bear predation, but was not limiting. Radio-marked calves between ~7-12 months of age had a survival rate of 0.67 and winterkill/parasite was the leading cause of mortality. Winter survival of calves was lower than in most populations in North America, although similar to areas with severe winter conditions. Calf survival during this time was highly dependent on late winter (18 February-4 May) mortality when 88% of deaths occurred. Winter survival (0.49) in 2002 was lower than in 2003-2004 (0.68-0.71).

Annual calf survival was estimated as 0.45, a rate lower than in populations with minimal predation like New Hampshire, and higher than in populations with high summer predation. The low annual survival of calves was related to high winter mortality associated with infestation of winter tick, not snow depth, forage restriction, or predation. Documentation of substantial tick-related mortality of radio-marked moose calves was unique to this study and when tick epizootics occur, specifically with other contributing factors (e.g., lungworm, poor body condition, winter severity), calf survival and recruitment could be <50%.

Winterkill/parasite mortality caused both low calf (0.49) and adult (0.85) survival

in winter 2002, whereas, calf survival was higher and no adult mortality occurred in winters 2003-2004. A high incidence of dead, winter tick-infested moose was also noted throughout northern New England in 2002. Unseasonably warm and snowless conditions in November and December 2001 probably increased the survival and transmission of winter ticks. Monitoring fall weather patterns could prove useful to forecast potential tick epizootics and abnormally high winter mortality of moose.

It is hypothesized that winter ticks may limit yearling production by reducing their winter survival and fitness as calves and their compensatory growth prior to fall as a yearling effectively increasing the age of first breeding. Winter ticks do not appear to reduce adult ovulation rates or body weight, but may influence productivity through reduced twinning. It has been suggested that yearling pregnancy rate and adult twinning rate may be influenced by similar factors, therefore, in this study the change in reproductive data could be an adaptive response to the stress associated with winter ticks. Tick infestations may also diminish body condition of pregnant cows resulting in smaller calves at birth; calf survival is believed to be related to birth weight which may predispose smaller calves to tick-related mortality.

Modeling with RAMAS (Ecolab v. 2.0) using a Leslie matrix design and incorporating survival rates and fecundity derived from radio-marked cows and reproductive data from harvested cows indicated that the population should have a positive finite rate of increase (λ=1.03-1.07), a rate lower than that associated with moose populations with adequate food, limited predation, and minor harvest. Substituting a slightly reduced winter survival rate of calves predicted a nearly stable growth rate (λ=1.01); a negative growth rate (λ=0.95) was predicted using both lower winter survival

of calves and yearling/adults. Survival of adult cows had the highest elasticity and sensitivity, but it was relatively constant in the population suggesting that winter survival of calves may be more important to annual population abundance although annual variability was not indicated in survival analysis. Despite this, tick epizootics influencing winter survival of both calves and adults most likely have primary importance to perceived population stability.

The physiological impact of blood removal by adult female ticks extends for approximately 8 weeks, and calves likely experience chronic, and eventually acute anemia during peak engorgement by weeks 4-6 during early-mid April. The metabolic exercise performed with conservative estimates indicated that total blood loss as a percent of total blood volume ranged from 27-48% and 64-112% for calves infested with moderate and severe tick loads during peak weeks 4-6, respectively. The percent of the daily metabolizable energy requirement required to replace the average daily blood loss during weeks 4-6 was 4.9-8.2% in a moderate infestation and 11.4-19.2% in a severe infestation. The protein deficit associated with blood loss and regeneration appeared to pose the most critical effect on calves. Daily protein loss during weeks 4-6 was 29-49% and 68-114% of the daily protein requirement during moderate and severe infestations, respectively. Daily protein losses of 50->100% occurred for 4 continuous weeks for severely infested calves.

The additional energy costs associated with compensating for blood loss would increase the daily energy deficit normal at end of winter, accelerate nutritional decline and weight loss when moose consume forage of minimal nutritional value, and likely cause increased physiological stress related to concurrent anemia. Heavily infested

calves are more susceptible to late winter mortality, however, the effect of a moderate infestation may be amplified by secondary infestations of lungworm, severe winters, and/or poor body condition.

Under current conditions, the perceived stability of the local moose population probably reflects the variation in survival, annual recruitment, and quite possibly low yearling fecundity caused by winter tick and more importantly epizootics. Although adult survival declined one winter of a tick epizootic, calf survival likely has the most impact because ticks have greatest and most frequent influence on calves. Furthermore, because no reproductive parameter or mortality factor was directly related to resource availability, current habitat quality is unlikely a limiting factor of the population.

This study indicated that ticks have a stronger influence on the moose population than predation, habitat, or human-related mortality factors. Ticks are more influential in years of high tick density such as 2002 when all age classes experienced mortality associated with parasitism and frequency of tick epizootics is the most important factor for managers. However, the high fertility, calving rate, and body condition of adult cows, as well as summer survival of calves should ensure population recovery after tick epizootics that periodically inhibit population growth. Management of moose in northern New Hampshire should include monitoring of spring and fall weather patterns to forecast potential and frequency of tick epizootics as well as spring mortality surveys to determine the extent of tick-related mortality.

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APPENDICES

APPENDIX A. NHFG/UNH MOOSE PROJECT NECROPSY DATASHEET.

NECROPSY REPORT PAGE 1
NH FISH AND GAME & UNH MOOSE PROJECT
P.O. BOX 173, MILAN, NH 03588
603-449-2094

Date of Report: _____
Filed by: _____

Ear Tag # _____ Frequency _____ NHFG Case # _____

Sex _____ Age Est. _____ Weight Est. _____

Date of last active signal: _____ By: _____

Date of mortality signal: _____ By: _____

Date of confirmed mortality: _____ By: _____

Date necropsied: _____ By: _____

Estimated date and time of death: _____

UTM coordinates: Zone: _____ E _____ N _____

Locality description: _____

CARCASS CONDITION: Fresh / Moderately decomposed / Badly decomposed / Dried – loose bones

PHOTOGRAPHS: Dorsal / Ventral / Lateral / Head / Internal / Site / Other _____

SAMPLES COLLECTED: Skull / Partial skeleton / Muscle / Fat / Bone marrow / Liver / Femur /Kidney / Lung / Heart / Brain / Eyes / Blood / Urine / Fecal / Endoparasites / Ectoparasites / Reproductive tract / Ovaries / Testes / Fetus / Incisor / Stomach contents / Hair /Hide
Other _____

Disposition of samples: _____

ADDITIONAL DATA AVAILABLE: Complete or partial measurements / External diagram / Antler measurements / Histology report / Toxicology report / Vet report

Other _____

REMARKS: _____

_____

_____

_____

HISTORY

SITE DESCRIPTION

Description:

Forest Size Class:Regeneration-Seedling / Sapling-Pole / Saw / Large Saw / Uneven

Forest Cover Type: Hardwood / Softwood / Mixed Hardwood / Mixed Softwood / Clearcut

Aspen-Birch / Nrthrn Hardwood / Swamp Hardwood / Spruce-Fir-Pine

Ground Vegetation: Sparse(<30% in 0-2ft zone) / Intermediate(30-75%) /Abundant(>75%)

Duff/Ground Layer: Wet, decaying logs / Rocky / Dead-Down Trees / Forest litter, moss

Type: Upland / Mid-slope / Lowland / Flatland / Wetland

Distance to: Moving water / Body of water / Swamp <50/50<100/100<200/>200m

Distance to: Paved / Unpaved Road <50/50<100/100<200/>200m

Distance to: Homes or camps <50/50<100/100<200/>200m

Snow depth:

Position of carcass:

Evidence animal has been in same area for some time Y / N:

Sign of other moose or additional moose tracks Y / N:

# of pellet groups and condition (more than one moose?):

Concentration of browsing: Y / N:

# of beds (more than one moose?):

Evidence of struggle, thrashing, circling behavior or slow death Y / N:

Signs of predation, presence of predators or scavengers (scat, tracks, etc.) Y / N:

Sign of human or vehicle tracks Y / N:

EXTERNAL

Collar condition: Both ear tags present:

Carcass condition: Fresh / Moderately decomposed / Badly decomposed / Dried – loose bones

Description:

Emaciated or bloated Y / N:

Signs of predation or scavenging on carcass (tooth punctures, claw marks, etc.) Y / N:

Blood, bruising or hemorrhaging in and around wounds Y / N:

Location & description:

Carcass covered with: Debris / Forest litter / Snow / Clean / Other, explain:

Hair/hide (color, areas broken/missing and %):

Light infection / Moderate infection / Severe infection / Very severe (Worst case)

Ticks present Y / N, distribution and % coverage:

Presence of other parasites / flies / maggots / fly eggs Y / N:

Location & description:

Scars / contusions / non-predation wounds / lesion or abscess Y / N: (Recent / Healing / Healed)

Location & description:

Collection of or discharge of body fluids or blood from carcass Y / N:

Location & description:

Human interaction Y / N: Bullet or other human related wounds Y / N:

Features / general condition / other:

Antler development: Calf Pedicles / Spike / Forked / Cervicorn / Med Palm / Lg Palm / Cast

Max spread:_____ # points left:_____ # points right:_____ beam diameter: _____

EYES, EARS, OTHER

PRIMARY INCISION

Inside carcass, to the touch: Hot / Warm / Cool / Cold / Frozen

Amount and type of fluid in abdominal cavity:

Abdominal worms present Y / N:

Muscle (muscle worm – 1mm whitish, elongated cysts present Y / N):

Areas of discoloration or hemorrhaging Y / N:

Fat content: cardiac, omental, perirenal, and subcutaneous (tail, head, and brisket) regions

No visible fat / slight fat / moderate fat / heavy fat

Viscera (positioned normally Y / N):

GASTROINTESTINAL TRACT

Mouth:

Obstructions Y / N: Browse present Y / N:

Mandible (lumpy jaw, distortion, tooth wear or misalignment):

Teeth:
bottom left:_____ # bottom right:_____ # top left:_____ # top right:_____

incisors:_____ # canines:_____ Age estimate:_____

Tongue and Esophagus:

Stomachs (rumen flukes present Y / N):

Rumen (ingestia):

Reticulum (honeycomb):

Omasum:

Abomasum (true stomach):

Small intestine, cecum & large intestine:

LIVER (Fascioloidiasis- "liver rot" or liver flukes present Y / N) (cysts present Y / N):

PANCREAS, SPLEEN OTHER

REPRODUCTIVE TRACT (If female, presence of pregnancy Y / N):

URINARY SYSTEM

Kidneys:

Urinary bladder:

CARDIOVASCULAR SYSTEM (Tapeworms or cysts present Y / N):

Heart:

Arteries, veins, etc.:

RESPIRATORY TRACT (Tapeworms or cysts present Y / N) (Lung nematodes present Y / N):

Trachea:

Bronchi:

Lungs:

Pneumonia signs (lungs heavy –solid not spongy, erratic color, fibrinous tags, abscesses):

NERVOUS SYSTEM (meningeal worm-"brain worm" present Y / N):

Brain (inflammation or brown/yellow tainted material):

Spinal column:

SKELETAL SYSTEM

Broken Bones or abnormalities Y / N:

Location and description:

Femur marrow condition & consistency: %FMF_____

White solid / Spotted pink solid / Dark pink solid / Yellow solid / Red solid / Red gelatinous / Yellow gelatinous / Yellow approaching gelatinous

OTHER

DIAGNOSIS POINTS

1.
2.
3.
4.

PROBABLE CAUSE OF DEATH: Malnutrition – Starvation / Winterkill-parasite / Vehicle collision / Capture-related / Hunting / Poaching / Undetermined

Explain: _____

_____

_____

_____

APPENDIX B. INDIVIDUAL MORTALITY OF RADIO-MARKED MOOSE IN NORTHERN NEW HAMPSHIRE, 2002-2005.

ID	Capture year	Sex	Mortality date[a]	Age[b]	%FMF[c]	Cause of death	Diagnosis
4	2001	M	23 May 02	1.0	63.5	Vehicle collision	Multiple fractures, internal trauma, slight body fat
7	2001	F	20 Jun 02	1.0	74.2	Vehicle collision	Multiple fractures, internal trauma, moderate body fat
9	2001	M	27 Apr 02	Calf	14.5	Winterkill/parasite	Malnutrition, very severe hair loss/damage, no body fat
13	2001	M	13 Dec 01	Calf	-	Capture myopathy	Moderate body fat, coyote scavenged
14	2001	F	20 Oct 06	5.5	-	Hunt	-
16	2001	F	18 Apr 02	15.5	10.7	Winterkill/parasite	Malnutrition, moderate hair loss/damage, no body fat, age
17	2001	F	12 Apr 02	1.5	52.2	Undetermined	Light hair loss/damage, slight body fat deposits
18	2001	F	19 Oct 02	2.5	-	Hunt	Heavy body fat
19	2001	F	22 Aug 03	3.0	92.5	Vehicle collision	Multiple fractures, internal trauma, heavy body fat
27	2001	F	17 Oct 04	4.5	-	Hunt	Heavy body fat
28	2001	F	20 Apr 02	6.5	12.4	Winterkill/parasite	Malnutrition, severe hair loss/damage, no body fat
32	2001	F	Winter 06	$\geq$9.0	-	Undetermined	Died after end of project; scattered bones
33	2001	F	Aug 06	$\geq$6.0	-	Vehicle collision	Died after end of project; not examined by project staff
34	2001	F	23 Oct 03	3.5	-	Hunt	Heavy body fat
35	2001	F	18 Jun 02	5.0	14.0	Undetermined	Malnutrition, severe hair loss/damage, no body fat
37	2001	F	21 Oct 03	4.5	-	Hunt	Heavy body fat
39	2001	F	21 Apr 02	12.5	65.9	Undetermined	Light hair loss/damage, moderate body fat
41	2001	F	30 Mar 02	Calf	11.1	Winterkill/parasite	Malnutrition, severe hair damage, no body fat, scavenged
42	2001	M	18 Apr 02	Calf	12.5	Winterkill/parasite	Malnutrition, very severe hair loss/damage, no body fat
45	2001	M	20 Feb 02	Calf	-	Winterkill/parasite	Malnutrition, moderate hair loss/damage, slight body fat
46	2002	F	16 Oct 04	4.5	-	Hunt	Not examined by project staff
126	2002	F	13 Jun 04	2.0	-	Vehicle collision	Not examined by project staff, hit I-95 Kennebunkport
127	2003	M	17 Oct 04	1.5	-	Hunt	Heavy body fat
128	2002	F	19 Jun 03	1.0	-	Vehicle collision	Multiple fractures
130	2002	M	19 Apr 03	Calf	41.1	Winterkill/parasite	Moderate hair loss/damage, light lungworm infestation, slight body fat, femur marrow-red gel despite %FMF
131	2002	M	10 Jan 03	Calf	-	Vehicle collision	Multiple fractures, internal trauma, heavy body fat

APPENDIX B. (CONTINUED).

ID	Capture year	Sex	Mortality date[a]	Age[b]	%FMF[c]	Cause of death	Diagnosis
136	2002	F	11 Apr 03	Calf	15.4	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat
142	2002	M	04 Dec 03	1.5	13.2	Undetermined	Malnutrition, no observed trauma, no body fat
144	2002	F	09 Oct 04	2.5	-	Vehicle collision	Not examined by project staff, hit I-95 Kennebunkport
145	2002	M	24 Dec 02	Calf	-	Vehicle collision	Multiple fractures
146	2002	M	09 Apr 03	Calf	11.2	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat, scavenged
148	2002	M	27 Mar 03	Calf	11.3	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat
149	2002	M	14 Oct 04	2.5	-	Hunt	Heavy body fat
150	2002	F	09 Apr 03	Calf	27.6	Winterkill/parasite	Malnutrition-red gel FMF, moderate hair loss/damage, moderate bot larvae infestation, slight body fat, June born
156	2003	F	28 Apr 04	Calf	13.7	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat, July born calf
157	2003	M	28 Apr 04	Calf	13.4	Undetermined	Malnutrition, only scattered bones and skin at site
158	2003	M	30 Apr 04	Calf	14.6	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat
165	2003	M	05 May 04	Calf	15.5	Winterkill/parasite	Malnutrition, moderate hair loss/damage, moderate lungworm infestation, no body fat
171	2003	F	14 Apr 03	Calf	13.7	Winterkill/parasite	Malnutrition, light hair loss/damage, moderate lungworm infestation, no body fat
173	2003	F	20 Apr 04	Calf	30.9	Vehicle collision	Multiple fractures, internal trauma, slight body fat
174	2003	F	20 Apr 04	Calf	12.3	Winterkill/parasite	Malnutrition, severe hair loss/damage, moderate lungworm infestation, no body fat
175	2003	F	25 Jun 05	2.0	-	Vehicle collision	Multiple fractures, internal trauma, heavy body fat

[a] Fate determined for some moose in 2006 after end of project, [b] Non calves aged with cementum annuli, [c] Femur marrow dried weight %.

APPENDIX C. INFORMATION AND FATE AS OF AUGUST 2005 FOR MOOSE CAPTURED IN NORTHERN NEW HAMPSHIRE, 2001-2003.

ID	Capture Year	Sex	Capture age	Last known fate	Notes
1	2001	F	Adult	Alive	Calf #163
2	2001	F	Calf	Dead	Capture death
3	2001	F	Calf	Collar drop	-
4	2001	M	Calf	Dead	Mother #36, sibling# 14
5	2001	F	Adult	Alive	Calf #150
6	2001	F	Calf	Collar drop	-
7	2001	F	Calf	Dead	Sibling #8
8	2001	M	Calf	Collar drop	Sibling #7
9	2001	M	Calf	Dead	Mother #25
10	2001	F	Calf	Uncollared	Mother #32, ear tagged, escaped
11	2001	M	Calf	Collar drop	-
12	2001	F	Calf	Collar drop	Mother #37
13	2001	M	Calf	Dead	-
14	2001	F	Calf	Dead[a]	Mother #36, in 2003 w/ calf after collar drop, harvested in 2006 hunt
15	2001	M	Calf	Collar drop	Mother #38
16	2001	F	Adult	Dead	GPS-collar, oldest aged-15.5 yr
17	2001	F	Yearling	Dead	GPS-collar
18	2001	F	Yearling	Dead	GPS-collar
19	2001	F	Yearling	Dead	GPS-collar
20	2001	F	Adult	Collar release	GPS-collar, calf #2
23	2001	F	Adult	Alive	Calves #45, 159
24	2001	F	Adult	Alive	-
25	2001	F	Adult	Alive	Calf #9
26	2001	F	Adult	Alive	Calf #156
27	2001	F	Adult	Dead	-
28	2001	F	Adult	Dead	-
29	2001	F	Adult	Alive	-
30	2001	F	Adult	Collar drop	Calf #162, drop as an adult
31	2001	F	Adult	Alive	-
32	2001	F	Adult	Dead[a]	Calf #10
33	2001	F	Adult	Dead[a]	-
34	2001	F	Yearling	Dead	-
35	2001	F	Adult	Dead	-
36	2001	F	Adult	Alive	Calves #4, 14, 118, 172, unmarked calf vehicle collision death
37	2001	F	Adult	Dead	Calves #12, 126, 140
38	2001	F	Adult	Alive	Calf #15

APPENDIX C. (CONTINUED).

ID	Capture Year	Sex	Capture age	Last known fate	Notes
39	2001	F	Adult	Dead	-
40	2001	F	Adult	Alive	-
41	2001	F	Calf	Dead	-
42	2001	M	Calf	Dead	-
43	2001	F	Adult	Alive	-
45	2001	M	Calf	Dead	Mother #23
46	2002	F	Adult	Dead	GPS-collar, darted in July
50/275	2002	F	Adult	Collar release	GPS-collar, darted in July
101	2003	F	Calf	Dead	Capture death, wrong colored ear tag for year
118	2003	M	Calf	Alive	Mother #36, sibling #172, wrong colored ear tag for year
119	2002	F	Adult	Alive	-
120	2002	M	Calf	Alive	-
125	2002	F	Adult	Collar release	GPS-collar
126	2002	F	Calf	Dead	Mother #37, sibling #140, killed on I-95
127	2003	M	Calf	Dead	Wrong colored ear tag for year
128	2003	F	Calf	Dead	-
129	2002	M	Calf	Alive	-
129	2003	M	Calf	Collar drop	Mother #133, drop as a 2 yr old, wrong colored ear tag for year
130	2002	M	Calf	Dead	-
131	2002	M	Calf	Dead	-
132	2002	F	Calf	Alive	-
133	2002	F	Adult	Alive	Calves #129 of 2003, #145
134	2002	F	Calf	Collar drop	Drop as a 2 yr old
135	2002	M	Calf	Collar drop	Mother #133, drop as a 2 yr old
136	2002	F	Calf	Dead	-
138	2002	F	Adult	Alive	Calf #165
139	2002	M	Calf	Alive	-
140	2002	M	Calf	Collar drop	Mother #37, sibling #126, drop as a ~2 yr old
141	2002	F	Calf	Alive	-
142	2002	M	Calf	Dead	-
143	2002	M	Calf	Collar drop	Drop as a 2 yr old
144	2002	F	Calf	Dead	Killed on I-95
145	2002	M	Calf	Dead	Mother #133
146	2002	M	Calf	Dead	-

APPENDIX C. (CONTINUED).

ID	Capture Year	Sex	Capture age	Last known fate	Notes
148	2002	M	Calf	Dead	-
149	2002	M	Calf	Dead	-
150	2002	F	Calf	Dead	Mother #5
152	2003	M	Calf	Collar drop	-
153	2003	M	Calf	Alive	-
154	2003	F	Calf	Alive	-
155	2003	F	Calf	Alive	Mother #119
156	2003	F	Calf	Dead	Mother #26
157	2003	M	Calf	Dead	-
158	2003	M	Calf	Dead	-
159	2003	M	Calf	Collar drop	Mother #23, drop as a 2 yr old
160	2003	F	Adult	Collar release	GPS-collar, calf #127
161	2003	F	Calf	Alive	-
162	2003	F	Calf	Alive	Mother #30
163	2003	F	Calf	Dead	Mother #1, capture death
164	2003	F	Calf	Collar drop[a]	-
165	2003	M	Calf	Dead	Mother #138
166	2003	M	Calf	Collar drop	Drop as a 2 yr old
167	2003	F	Calf	Alive	-
168	2003	F	Calf	Unknown	Disappeared July 2005
169	2003	F	Calf	Alive	Sibling #174
171	2003	F	Calf	Dead	-
172	2003	M	Calf	Collar drop[a]	Mother #36, sibling #118
173	2003	F	Calf	Dead	-
174	2003	F	Calf	Dead	Sibling #169
175	2003	F	Calf	Dead	Collar, killed as a 2 yr old and lactating

[a] Fate determined after end of project.

APPENDIX D. INSTITUTIONAL CARE AND USE COMMITTEE APPROVAL FORM.

UNIVERSITY of NEW HAMPSHIRE

June 30, 2005

Peter Pekins
Natural Resources
James Hall
Durham, NH 03824

IACUC #: 040704
Original Approval Date: 07/21/2004 **Next Review Date:** 07/21/2006
Review Level: A

Project: Moose Habitat Use and Mortality Assessments in New Hampshire

The Institutional Animal Care and Use Committee (IACUC) has reviewed and approved your request for a time extension for this protocol. Approval is granted until the "Next Review Date" indicated above. You will be asked to submit a report with regard to the involvement of animals in this study before that date. If your study is still active, you may apply for extension of IACUC approval through this office.

The appropriate use and care of animals in your study is an ongoing process for which you hold primary responsibility. Changes in your protocol must be submitted to the IACUC for review and approval prior to their implementation.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Roger E. Wells, D.V.M.
Vice Chair

cc: File

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building, 51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564